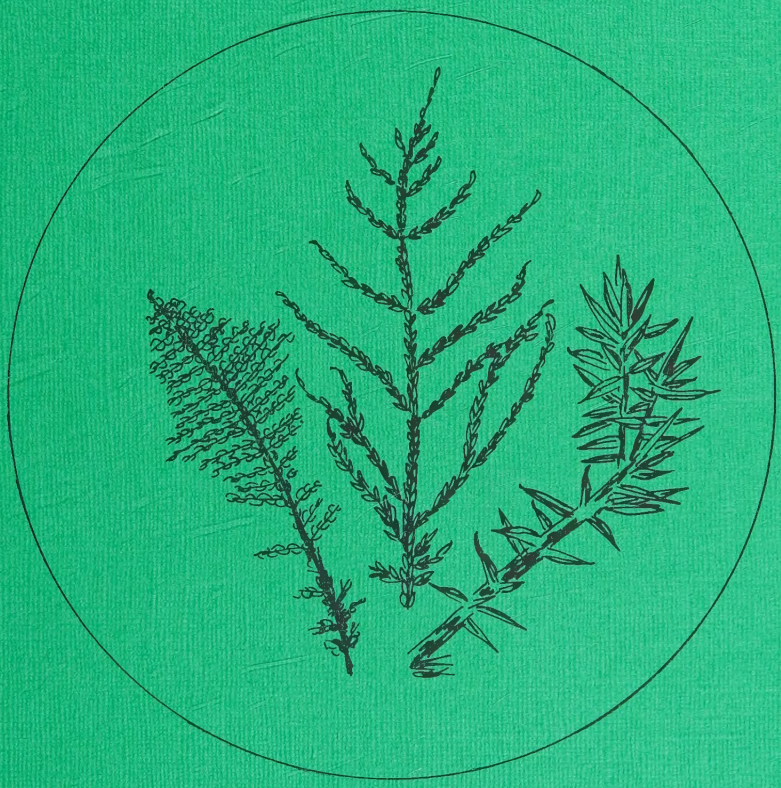
PHOTOSYNTHESIS, GROWTH AND COMPETITIVE ABILITY OF SOME CONIFEROUS FOREST MOSSES AND THE INFLUENCE OF HERBICIDES AND HEAVY METALS (Cu , Zn)



INGRID STJERNQUIST
DEPARTMENT OF PLANT ECOLOGY
UNIVERSITY OF LUND, SWEDEN

LUND 1981

PHOTOSYNTHESIS, GROWTH AND COMPETITIVE ABILITY OF SOME CONIFEROUS FOREST MOSSES AND THE INFLUENCE OF HERBICIDES AND HEAVY METALS (Cu, Zn).

I. Stjernquist, I.1981. The influence of nutrient and climatic variables on the field CO_2 assimilation of Pleurozium schreberi and Dicranum polysetum and their effect on seasonality of growth.

II. Stjernquist,I.1981. Growth and carbon balance of two coniferous forest moss species.

III. Stjernquist, I & Ingelög, T.1981. Effects of silvicultural herbicides on the photosynthesis of seven moss species.

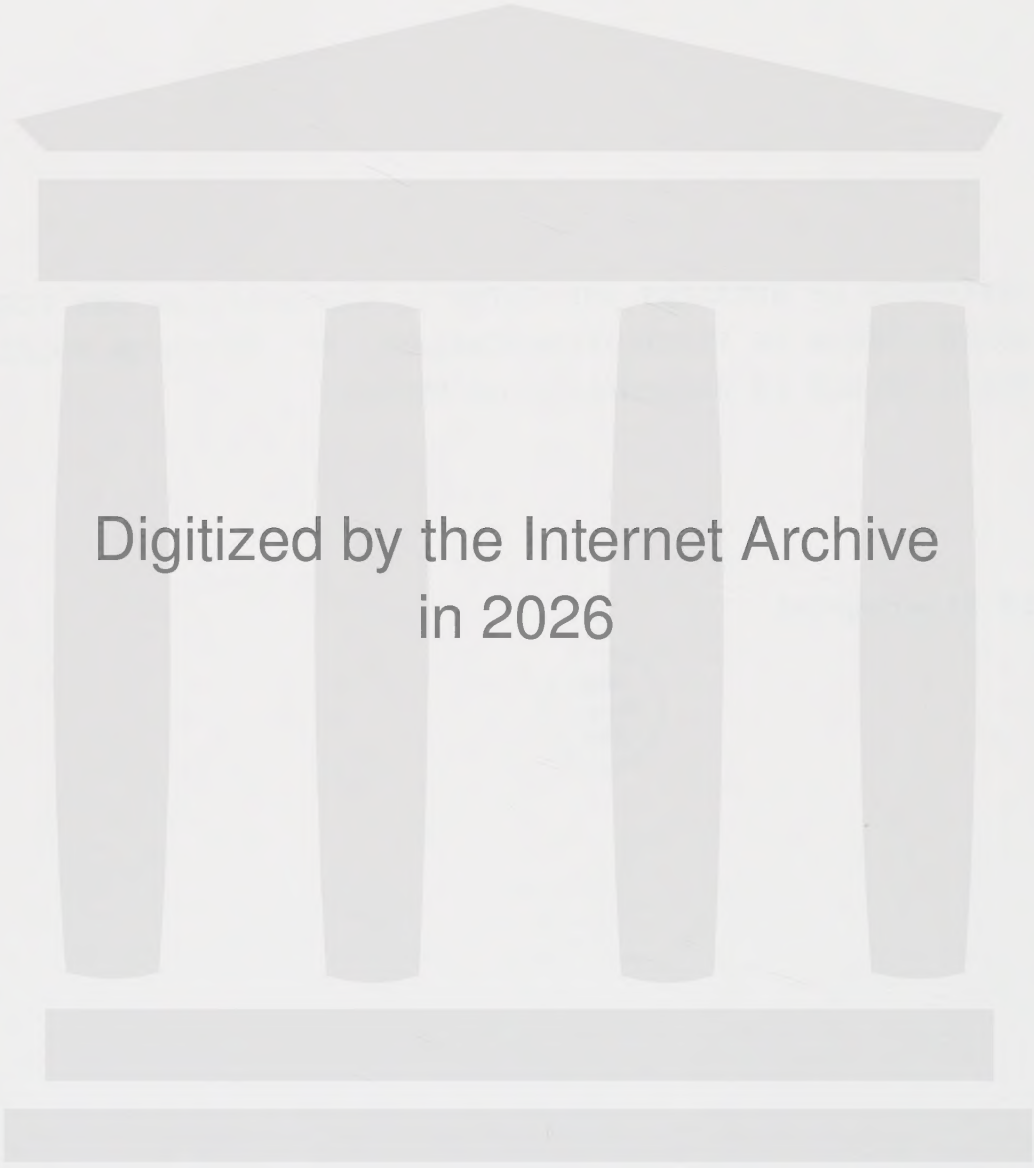
IV. Stjernquist, I.1981. Influence of Cu and Zn deposition on photosynthesis and growth of two moss species.

UNIV.
LEIDEN
BIBL.

THE INFLUENCE OF NUTRIENT AND CLIMATIC VARIABLES ON THE FIELD CO_2 ASSIMILATION OF PLEUROZIUM SCHREBERI AND DICRANUM POLYSETUM AND THEIR EFFECT ON SEASONALITY OF GROWTH.

Ingrid Stjernquist

Dept. of Plant Ecology
Helgonavägen 5
S-223 62 LUND
Sweden


Digitized by the Internet Archive
in 2026

https://archive.org/details/IA41553418_0003

ABSTRACT

The effect of environmental variables on the diurnal variation in CO_2 assimilation of Pleurozium schreberi (Brid.) Mitt. and Dicranum polysetum Sw. was studied in situ in two forest stands in Central Sweden, one 120-year-old (Ih V) and one 20-year-old (Ih II), in July and August 1976 and 1977 and November 1977. The experimental area of Ih II was divided into control, irrigated and irrigated + fertilized plots. Dicranum has the highest assimilation in dry conditions, maximum 0.9 mg CO_2 g $dw^{-1}h^{-1}$ and in November when light intensity was low, 1.1 mg CO_2 g $dw^{-1}h^{-1}$. After rainfall or irrigation the CO_2 fixation of Pleurozium is 2-3 times that of Dicranum, with a maximum value of 4 mg CO_2 g $dw^{-1}h^{-1}$. The Ih V plot was placed beneath a closed pine canopy and in August the two moss species appeared to have the same assimilation rate. In July the values were very low and in the morning significantly higher for Dicranum. Both bryophytes showed greater differences in CO_2 incorporation between habitats than between years. Fertilization with complete fertilizer indicates that growth of Pleurozium and Dicranum is limited by supply; assimilation was stimulated to the same extent. Following fertilization the moss shoots decrease their capacity to retain water and especially Pleurozium changed growth form to erect shoots without branches. The chlorophyll content of the two species does not appear to be influenced by varying water conditions. At Ih V Pleurozium has a value twice that of the control at Ih II. Fertilization increased the chlorophyll content two-fold and three-fold for Dicranum and Pleurozium, respectively. Higher nutrient supply is suggested to alter the competitive relations between the mosses only in shaded habitats or when the Pleurozium shoots changed growth form. Of the climatic variables, air humidity and irradiation seem mainly to control the assimilation rates of Pleurozium and Dicranum. The importance of these factors for bryophyte distribution and seasonality of growth is discussed.

1 INTRODUCTION

Pleurozium schreberi and Dicranum polysetum are the dominant moss species in many coniferous forests. They are also abundant in open areas, e.g. in clear-cuts and on heaths. Pleurozium is the most wide-spread species of the two, also being found on bogs and in the mountains (Nyholm 1954-69). The niches of the two bryophytes seem to be very close since shoots of Pleurozium and Dicranum often grow intertwined.

The distribution and competitive ability of a moss species are supposed to be largely controlled by combined effects of environmental variables. The reciprocal order of precedence of these variables in situ has been little analysed. Lee and La Roi (1979) have studied the joint influence of altitude and moisture on the distribution of bryophytes. They infer that bryophytes are the most responsive to moisture-related factors.

Seasonality of bryophyte growth has earlier been discussed in relation to vegetative elongation of the shoots. One annual growth period has been identified in experimental areas with maritime climate (Lackner 1939, Tallis 1959, Longton & Green 1969, Pitkin 1975) and two periods in those of a more continental climate (Hagerup 1935, Kallio & Heinonen 1975, Watson 1975). Increase in length has often been observed to occur during the wettest months of the year. There is, however, no direct relationship between the photosynthetic capacity of mosses and their increase in length. Hoffman (1966) has observed that dark habitats produce taller and thinner shoots of Funaria hygrometrica(Hedw.). Hylocomium splendens (Hedw.) Br.Eur. has a period of shoot elongation in summer, but the increase in dry weight is also high during autumn (Tamm 1953).

Because most moss species lack internal conductive tissue to translocate nutrients from below, the nutrient supply to the bottom layer is assumed to be related to the ion concentration in precipitation and in leachates from trees and litter (cf. Tamm 1953, Callaghan et at. 1978, Longton & Green 1979).

If both water supply and nutrients are limiting to bryophyte growth, the importance of the variables may be difficult to separate.

The aim of the present study was to analyse the following questions:

- Does increased nutrient supply influence the photosynthetic process and production of Pleurozium and Dicranum, respectively?
- Do environmental variables significantly control CO_2 assimilation of Pleurozium and Dicranum and if so are there any differences between the species in different kinds of habitats?
- Can the variables effect the distribution of Pleurozium and Dicranum?
- Does any general seasonality of growth exist, expressed as increase in dry weight and, in that case, which factors are important for establishing oscillation?

2 MATERIALS AND METHODS

2.1 Site description

The investigation was conducted during the years 1976-1977 at Ivantjärnsheden, Jädraås Ecological Research Station in Central Sweden (60°49'N, 16°30'E). The experimental area consisted of one 20-year-old (IhII) and one 120-year-old (Ih V) stand of Scots pine (Pinus sylvestris L.). The vegetation in the stands was of a lichen-dwarf-shrub type (Ebeling 1978). For further description of the stands see Axelsson & Bråkenhielm (1980) and Bråkenhielm & Persson (1980). The experimental plots on IhII were parts of an irrigation and fertilization investigation that started in 1974 (Aronsson et al. 1977). IhII was divided into five randomized blocks, each containing four parcels with different treatments. The bryophyte study was accomplished in blocks Nos. 1 and 5 and in the following parcels:

C = Control
I = Diurnal irrigation during vegetation period (ca 2.5 mm a day)
IF = Diurnal irrigation plus fertilization with complete fertilizer (Ingestad 1967).

Irrigation and fertilization took place daily (May-Sept.) at about 5 o'clock in the morning. The liquids were distributed over the plots by sprinklers and the maximum amount each day was 3 mm. In 1976-77 the IF-parcels were totally supplied with 15g N m^{-2}, 10g P m^{-2} and 2g K m^{-2} per year. The annual input with bulk rainfall amounted to 0.31g N m^{-2} and 0.05g K m^{-2}. The amount of P was insignificant (Bringmark 1977).

2.2 Material and experimental time

Pleurozium schreberi (Hedw.) Brid. and Dicranum polysetum Sw. were the dominant moss species in the bottom layer of both IhII and IhV. Their appearance and occurrence differed between plots and treatments (Table 1).

Variations in gross photosynthesis and micro-climate during representative days in July and August 1976 and 1977 were studied in parallel at IhII block 1 and IhV. Measurements at IhII were made only in August 1977, block 5, and in November 1977, block 1. The effect of a thick field layer of Chamaenerion angustifolium L. on the photosynthetic process of the experimental bryophytes was studied on the IF-plot in August 1977. Samples for determination of water content and chlorophyll concentration of the species were determined at IhV and IhII and were taken at noon, August 18, 1977.

An experimental plot, 2 x 2 m, was selected in every stand and treatment. Inside the plots, the moss shoots were randomly selected for measurement of assimilation rate. Each sampling for assimilation determination contained 5 parallels of each moss species. Chlorophyll concentration was estimated from a composite sample consisting of 5 parallels collected as above.

2.3 Measurement techniques

The assimilation rate was determined as incorporation of $^{14}CO_2$ according to Shimshi (1969). The uppermost 2 cm of the moss shoots were exposed to $^{14}CO_2$ for 20 seconds and then immediately frozen

in liquid nitrogen. Combustion of the samples was accomplished with a Packard Tri Carbonate Sample Oxidizer (Model 306) after dry weight determination (85°C, 24 hours). The radioactivity was measured in a liquid scintillation counter (Intertechnique SL 30).

Irradiation, temperature and relative humidity during the investigation periods were obtained from the climatic stations on IhII and IhV (Perttu et al. 1980). Supplementary measurements of irradiation and temperature just above the moss carpet were accomplished simultaneously with measurements of assimilation rate. Irradiation was registered with a quanta sensor, Lambda 400-700 nm, and temperature with a thermistor, Mavotherm. In August and November 1977, the relative humidity was measured with a psychrometer.

The chlorophyll concentration was determined according to the method described by Lindner (1974) and the water content of the moss shoots as the difference between fresh and dry weight (85°C, 24 hours).

2.4 Calculations and statistics

The diurnal CO_2 assimilation for each treatment and month was estimated by interpolation between the measurement points and integration of the area under the resulting curves.

Analysis of variance was used to test the significance of the correlation between the assimilation rates of Pleurozium and Dicranum, respectively, and each of the variables irrigation, vapour pressure deficit and temperature as well as the influence of shading. The figures were obtained from the IF-plot in August 1977. All effects are assessed simultaneously, with each effect being adjusted for all other effects.

In order to determine the rank of importance of the climatic variables, these were used as independent variables in a step-wise linear regression analysis using the assimilation rate of both

moss species as the dependent variables. For both test methods the material was separated into a morning and an afternoon group according to Figure 1.

3 RESULTS

3.1 Diurnal variation of assimilation rate

The assimilation rates of Pleurozium and Dicranum at different times of the year are illustrated in Figures 2-5. The weather conditions on the actual measurement days are shown in Table 2.

3.1.1 The 120-year-old stand

In July the rate of CO_2 assimilation was very low for both Pleurozium and Dicranum and the differences between the two years were small. In the morning of July 1976 there was a significantly higher photosynthetic capacity in Dicranum than in Pleurozium, ($p < 0.001$, Figure 1a). The measurements in July 1977 were preceded by a drought period with a relative humidity beneath 100% even at night (Figure 1c). Both species had an insignificant assimilation rate during the whole day.

In August gross photosynthesis curves of the two bryophytes followed each other closely from sunrise to noon in accordance with irradiation (Figure 1b, d). The maximum rate was 2 mg $CO_2 g\ dw^{-1} h^{-1}$.

3.1.2 The 20-year-old stand

On the control plot Pleurozium and Dicranum showed very low or insignificant photosynthetic capacity during clear summer days (Figures 2-4). Decreased irradiation in August 1977 gives a maximum assimilation rate of 0.9 mg $CO_2 g\ dw^{-1} h^{-1}$ for Dicranum, which is significantly ($p < 0.01$) higher than for Pleurozium (Figure 4). After rainfall the CO_2 fixation of Pleurozium increased to 4 mg $CO_2 g\ dw^{-1} h^{-1}$, three times higher than for Dicranum (Figure 3).

The investigations in November showed maintained photosynthesis at the end of the vegetation period. The assimilation rate of both moss species followed the variations in irradiation quite well, with a maximum at noon, but Dicranum had the significantly higher value ($p < 0.001$).

On the irrigated plot the variations in photosynthetic capacity more closely followed the irradiation (Figures 3-5). In summer, when irradiation was moderate, the assimilation rate of Pleurozium increased as compared to Dicranum and in August 1977 it was twice as intense. In November, with low light intensity and low vapour pressure deficit, no differences between the moss species could be seen.

Irrigation and fertilization increased the assimilation rate of the moss species more than irradiation alone. The highest activity, 8 mg CO_2g $dw^{-1}h^{-1}$, was measured for Pleurozium in August 1976 and 1977 (Figures 4-5). In summer the bryophytes were more active during the morning periods, but an inhibition of assimilation very soon appeared, especially on days with high vapour pressure deficit (Figure 2). In November the gross photosynthesis of Dicranum was favoured.

3.2 Diurnal carbon incorporation

Among the untreated plots (IhII : C and IhV), the highest amount of total CO_2 incorporated was noted in the mature forest both for Pleurozium and Dicranum (Figure 5). Differences between the years are greater than between species. In November, however, Dicranum has the highest CO_2 incorporation, 5 mg gdw^{-1}, and the assimilation of both moss species was on the same level as for the irrigated plot. Irrigation in summer promoted the diurnal CO_2 fixation especially for Pleurozium, but at high irradiation conditions - or at least 1500 µE, Dicranum was the most efficient bryophyte. Fertilization and irrigation increased the carbon fixation two-fold, compared to levels at IhII:I in August and November, but in July only Pleurozium was stimulated.

3.3 Water content and appearance of the moss shoots

The growth form and morphology of the Pleurozium and Dicranum shoots are summarized in Table 2. With high nutrient supply the shoots became thinner and taller. Pleurozium lost nearly all lateral branches and also changed growth form, from loose mats to dense tufts of erect individuals.

A higher water content in the shoots of Dicranum as compared to Pleurozium was characteristic for all experimental plots (Figure 7). The difference was especially evident in the old pine stand. The moss shoots on the I-plot contained more water than those on the IF-plot in spite of the identical water supply.

3.4 Chlorophyll content

On IhII, the chlorophyll content of Pleurozium and Dicranum was of the same order in both control- and irrigated plots (Figure 7), and the differences between the species were insignificant. Fertilization caused an increase in chlorophyll concentration to values twice and three times that of the control plots for Dicranum and Pleurozium respectively, but the shading of the thick Chamaenerion layer decreased the chlorophyll content of the mosses as compared to the open area. On IhV, beneath the closed tree canopy, the value for Pleurozium was twice that of the non-fertilized plots in IhII, but Dicranum was not appreciably affected.

The assimilation rate per unit of chlorophyll in August increased with fertilization for Dicranum (Figure 8). Pleurozium, however, had the opposite reaction. Low irradiation, 40 µE, depressed the activity of the species to about 3 mg CO_2 mg $chl^{-1}h^{-1}$. With normal nutrient supply Dicranum on IhV had a maximum assimilation rate of 6 mg CO_2 mg $chl^{-1}h^{-1}$, which was of the same order as on the fertilized unshaded plot and about three times the Pleurozium value.

3.5 Influence of environmental variables

When nutrient supply was non-limiting for photosynthesis, the assimilation rate of Pleurozium in the morning, expressed as mg CO_2 per unit dry weight, was significantly controlled by the three climatic variables irradiation, temperature and vapour pressure deficit (Table 3). The highest correlation, $p < 0.001$, existed between assimilation and irradiation. During the second part of the day, irradiation, vapour pressure deficit and the shading factor seemed to be important to a similar degree, $p < 0.001$.

The step-wise regression for the period shows that the assimilation of Pleurozium primarily depends on variations in air humidity (Table 4).

The regression equation is estimated to be:

$A = 3.46 - 0.31H + 0.002I$

where A = assimilation rate, expressed as mg CO_2 g dw^{-1}

H = vapour pressure deficit; mbar

I = irradiation, $\mu E \cdot m^{-2} s^{-1}$.

During the morning the assimilation rate of Dicranum was only correlated to irradiation (Table 3). As in Pleurozium, the assimilation of Dicranum during the second part of the day was highly significantly ($p < 0.001$) related to all the three variables, irradiation, vapour pressure deficit and shading. Totally, irradiation was the most important variable in controlling the CO_2 fixation of Dicranum (Table 4).

The regression equation is estimated to be:

$A = 2.42 - 0.23H + 0.003I$

using the symbols as above.

4 DISCUSSION

4.1 Methods

Investigations of the photosynthetic response of bryophytes to environmental variables have mainly used dry weight as the base for expressing gross and net assimilation rate. Sestak et al. (1971) stated that for maximal information photosynthesis must be related to a characteristic which controls the process. In investigations with vascular plants the projected leaf area is the most frequently used unit. For many moss species a correct estimation of the leaf area reached by irradiation is difficult to provide because the great number of leaves more or less cover each other, depending on species. Some of the coniferous forest mosses, e.g. Pleurozium, also have very thin leaves and the irradiation, penetrating the upper leaf layer, may probably be enough for even the lowest leaves to photosynthesize.

Photosynthetic rate, as expressed per unit of chlorophyll, would be a suitable base if the absorption of energy was limiting for the process. However, bryophytes occupying the forest floor reach their optimal photosynthesis at relatively low light intensity (cf. Stålfeldt 1937). Under conditions of high irradiation the assimilation rate in situ may also be limited by other variables, e.g. water content (Figure 8a). Another problem when using an isotope method for estimating photosynthesis is that the measurements of chlorophyll concentration and assimilation must be performed on separate shoots.

Apart from dry weight theoretically being inferior as a base, because no direct relationship exists with the photosynthetic process, the restrictions discussed above still make it the most suitable unit for moss investigations in situ. The plexiglass cuvette used for ^{14}C-fixation allows about 2 cm of the youngest tissue to be equally exposed to the irradiation intensity at the top of the moss carpet. Depending on species, the most photosynthetically active segment of coniferous forest bryophytes has been reported to be 0-1 or 1-2 cm from the apex, but totally

3-4 cm of the shoots are able to photosynthesize *in situ* (cf. Bates 1979, Stjernquist 1981). Combining values for assimilation capacity and biomass will thus give an overestimation of the photosynthetic rate per unit of ground area for the two species.

4.2 Effect of nutrient supply

The stimulated photosynthetic capacity at high nutrient input indicates that the growth of *Pleurozium* and *Dicranum* at control and irrigated sites at Ivantjärnsheden are limited by nutrient supply. When the moss carpet is affected by a canopy, assimilation rate during varying periods of the year may then be influenced by ion uptake from throughfall. The nutrient concentration in precipitation is especially high after dry periods, which at Ivantjärnsheden are most frequent in summer (Aronsson *et al.* 1977). Because bryophyte layers are assumed to absorb a maximum of a few mm of rain, a high evaporation and an extended water input from the canopy may also increase nutrient uptake in the moss shoots. The significantly ($p < 0.01$) higher assimilation rate of *Dicranum* at IhV in July 1976 may be the result of increased nutrient supply, because climatic conditions are identical at IhII and IhV (Figure 1a, 2a). A stimulated photosynthesis in summer beneath one of the other vegetation layers is assumed to be important for total annual CO_2 fixation, as it may partly compensate for the small irradiation intensity in autumn.

Tamm (1953) reported from field studies on *Hylocomium splendens* in mature coniferous forests that nutrient uptake closely followed growth, when irradiation was at least 50% of that in the open field. Further, he stated that the highest productivity exists just outside the projections of the tree crowns where maximum throughfall is received. In contrast to the results of Tamm, Skre & Oechel (1979) found a negative or insignificant effect on annual growth of *Hylocomium* and *Pleurozium*, expressed as dry weight per shoot, after fertilization with nutrient solutions two to five times the normal input from rain.

The continuous fertilization at IhII seemed to stimulate diurnal CO_2 assimilation of the two moss species to the same extent. An important effect of fertilization for both species was probably the increased chlorophyll content. Berg (1975) has stated that the chlorophyll concentration in bryophytes on Hardangervidda, Norway, was controlled by water and/or nutrient supply. At Ivantjärnsheden, only fertilization had any influence on the chlorophyll concentration of the two mosses. The high assimilation capacity of fertilized Pleurozium shoots seems only to be dedendent on chlorophyll increase, since CO_2 fixation per unit of chlorophyll decreases at maximum photosynthesis by about 20%. With Dicranum, however, the positive reaction seems to be a combined result of both a higher chlorophyll content and a higher efficiency.

Changes in in situ productivity of Pleurozium and Dicranum populations may also be determined by varying nutrient supply in a more indirect way. The shoot density per unit of ground area increased, which caused a change in growth form of Pleurozium. It turned into a more tufty growth and the shoots almost lost their lateral branches. This is likely to have decreased the irradiation penetration of the moss carpet, and probably only the top centimetre of erect shoots was able to utilize its entire photosynthetic potential. When the whole shoot is exposed, this top centimetre accounts for about 30% of the total assimilation and the photosynthetically most active segment is 1-2 cm from the apex (Stjernquist 1981). The assimilation potential per unit of dry weight, given in Figure 6 for Pleurozium, is thus probably considerably higher than the in situ diurnal CO_2 fixation. This is emphasized by the fact that Pleurozium has a high irradiation optimum for photosynthesis. The reduced ability may be most evident in autumn when irradiation intensity decreases. Another factor counteracting the stimulation effect of fertilization may be the reduced ability of the thin Pleurozium shoots to preserve water during the day, especially at high vapour pressure deficit. The assimilation rate of fertilized shoots, therefore, will be inhibited at an earlier time of day

compared to shoots of normal appearance (Figure 3b, 5).

Dicranum, with about 50% of assimilation capacity in the top centimetre and with normally erect growth form, may actually be stimulated by the high fertilization and the magnitude is assumed to be close to the potential value given in Figure 6.

Increased nutrient supply does not seem to alter the competitive relations between Pleurozium and Dicranum, as long as the ion concentration does not result in a changed growth form for Pleurozium. However, in habitats shaded by a closed canopy, where the chlorophyll content of Pleurozium already has increased, fertilization probably favours Dicranum.

4.3 Influence of environmental variables

Irradiation and air humidity appear to be the major environmental variables controlling the gross photosynthesis of Pleurozium and Dicranum during summer conditions, when the mosses dry out during the day. In rainy periods, temperature may also be influential for Pleurozium, since a statistically significant ($p < 0.05$) positive relation between temperature and assimilation rate was found for the morning period after irrigation. A positive correlation between temperature and stem elongation at otherwise constant climate has been reported by, e.g. Longton & Green (1979) with irrigated Pleurozium shoots.

The above results were achieved in an experimental situation, when the temperature during the photosynthetically active hours was above $10^{\circ}C$, and their validity at lower temperatures is not indisputable. Temperature can probably be of greater importance under cooler and moister conditions, e.g. in autumn, when evaporation decreases.

There was also a negative influence of the "shading factor", i.e. a reduced assimilation rate of both moss species in shaded habitats, besides the immediate effect of lower light intensity. This influence could only be seen during the desiccation phase and

probably depended on several factors, notably a decreased chlorophyll content. For Pleurozium this is combined with a reduced assimilation efficiency of the photosynthetic apparatus as well, as indicated by the lower assimilation rate per unit of chlorophyll.

The differences in photosynthetic response between Pleurozium and Dicranum to environmental variables may be summarized as follows:

1) Air humidity is the main controlling factor for assimilation rate of Pleurozium, but during short periods with optimal water supply, the amount of incorporated CO_2 is highly dependent on the irradiation. In this situation, even temperature affects the assimilation rate to a smaller degree.
2) The photosynthetic activity of Dicranum is mainly controlled by irradiation and only heavy desiccation makes the air humidity factor significant.

Water

The effect of desiccation on assimilation rate of Pleurozium and Dicranum growing in undisturbed carpets may be illustrated by data from the gradient in water availability IhII:C < IhV < IhII:I. The bryophytes on the two IhII plots are exposed to identical air humidity, but the daily irrigation of IhII:I in summer resulted in a water content in the shoots being high and extending the period of assimilation on dry days. Both Pleurozium and Dicranum, e.g., had a water content of about 400% of the dry weight in August 1977, a value above optimal for photosynthesis of the related Dicranum majus, as estimated by Dilks & Proctor (1979). Desiccation of IhII:C in summer is probably at the lower limit for survival of the two moss species. Pleurozium, the dominating bryophyte at IhV, only grows in the neighbourhood of Calluna clones, and Dicranum is distributed in small scattered populations over the area.

The photosynthetic reaction of a single shoot of a certain moss species to decreased humidity and periods of continuous desiccation is assumed to depend on water content (cf. Peterson & Mayo

1975, Callaghan *et al.* 1978, Dilks & Proctor 1979, Tobiessen et al. 1979) and the physiological resistance to desiccation (cf. Hinshiri & Proctor 1971, Nörr 1974, Brown & Buck 1979). For bryophytes with no internal water conduction, water content is related to air humidity (cf. Tobiessen et al. 1979).

The ability of *Pleurozium* and *Dicranum* populations to grow and survive in the habitats along the water gradient may be determined not only by the water-holding capacity of the single shoot (cf. section 4.2) but also by the undisturbed moss carpets (Figure 7). In habitats with water supply from precipitation only, the water content of *Dicranum* shoots is higher compared to that of *Pleurozium* in the middle of a summer day. This may be related to the fact that *Dicranum* tufts are able to maintain higher humidity around the shoots than the loose *Pleurozium* mats. The dense growth form of *Dicranum* therefore allows a longer assimilation period during the day. Källomäki & Hari (1976) stated that because of the water-holding capacity of a moss carpet, it is hardly likely that photosynthesis will cease, even during longer periods of drought. *Pleurozium* and *Dicranum* in non-irrigated habitats, however, are dependent on a relative humidity of 100% and dew formation at night for assimilation. If not, both species attain an insignificant assimilation during the following day (cf. Figure 2c, 3b). The assimilation rate in the morning also seems to be correlated to the number of moist hours at night (Figure 3a, 5a).

The unchanged chlorophyll content of *Pleurozium* and *Dicranum* on the extreme habitats, IhII:O and IhII:I, indicates that desiccation under natural conditions does not influence the chlorophyll content of the two species. Dilks & Proctor (1974) found for the related moss *Hylocomium splendens* that chlorophyll content did not decrease until relative humidity has been as low as 32% continuously throughout seven days. Because of dew formation during most nights, longer unbroken dry periods probably do not exist in the forest ecosystems.

The small amount of incorporated CO_2 and the inhibited assimilation rate during summer days with no precipitation in the driest habitat may not be dependent on an irreversible damage to the photosynthetic apparatus of Pleurozium and Dicranum. Following heavy rain on August 26, CO_2 assimilation of the two bryophytes was not depressed compared to irrigated mosses.

Irradiation

The close correlation between the assimilation rate of Pleurozium and irradiation at good water supply seems to be an important feature of the photosynthetic ability of this bryophyte. In open habitats with high irradiation, Pleurozium is able to increase assimilation rate to a value twice that of Dicranum (Figure 4). This is contradictory to the results of Källomäki & Hari (1976), who stated that the photosynthetic activity of Pleurozium is lower compared to other coniferous forest mosses, independent of irradiation intensity.

In all the non-fertilized sites the maximum assimilation rate in summer for moist Dicranum shoots was about 2 mg $CO_2 \cdot g\ dw^{-1}$. Even if CO_2 fixation is mainly controlled by variations in irradiation, Dicranum may be unable to utilize high irradiation intensity to the same extent as Pleurozium. The decreased irradiation in autumn, however, probably favours the growth of Dicranum during that period.

The two moss species react very differently when growing under a closed tree canopy. The results indicate that the photosynthetic activity of Pleurozium may be negatively affected by a shading vegetation layer. Evidently the moss seems to be able to compensate the reduced assimilation per unit of chlorophyll with increased chlorophyll content, but totally the CO_2 fixation, when unlimited by desiccation, is of the same magnitude as for Dicranum in summer. Huddinott & Bain (1979) showed that the quality of light changed as it passed through the canopy and that this change causes similar reactions for some coniferous moss species, but also that the growth responses are specific for a certain bryophyte.

A comparison of the photosynthetic reactions of Pleurozium and Dicranum to varying irradiation and humidity conditions give special characteristics to the moss species in question that may be of importance for their distribution.

1. The CO_2 incorporation of Pleurozium may be promoted in moist habitats by a high irradiation and in protected ones by an open canopy, which does not significantly change the light quality but inhibits the evaporation rate, e.g. in forest glades.

2. The CO_2 assimilation of Dicranum seems to be less sensitive to dark or dry habitats than that of Pleurozium. In such habitats Dicranum will be favoured.

The similar competitive ability under a closed canopy probably explains why the two species often grow intertwined in mature forests.

4.4 Seasonality of growth

The characteristic reactions of Pleurozium and Dicranum to environmental variables discussed in section 4.3 make it possible to hypothetically describe the variations of CO_2 fixation in the moss layer for the three habitats at Ivantjärnsheden along the water gradient during the whole vegetation period from the middle of May to November. In May, in connection with melting of snow, the high irradiation together with cool and moist nights may give rise to an assimilation in the open areas of the same magnitude as on IhII:I in August. In the dry habitat, assimilation for both moss species soon decreases to the minimum shown by Figure 6, because the climate at Ivantjärnsheden in early summer is rather dry (Aronsson et al. 1977). Decreased evaporation and ample dew formation at night in late August will again stimulate CO_2 incorporation and reach maximum values in September. In October, assimilation decreases depending on low irradiation intensity and few photosynthetically active hours.

In the habitat with a good water supply, Dicranum probably has about the same CO_2 fixation from May to October which is largely

controlled by irradiation intensity. Pleurozium, however, seems to have two moderate maxima, one in May and one in late August.

Under closed canopy, variations in CO_2 incorporation may by similar to the dry open habitat, but with smaller oscillations.

Calculations of seasonality of growth from the assimilation values must take into account respiration rate and the shading effect of litter fall. The respiration losses for moss species growing in coniferous forests in the examined temperature range, 10-25°C, seem to be small for shoots with optimal water content, about one-tenth of assimilation (Dilks & Proctor 1975). The sharp burst of respiration after a longer period of continuous desiccation reported by several authors (cf. Hinshiri & Proctor 1971, Peterson & Mayo 1975) is probably not so abrupt and long-lasting in natural conditions, because the number of hours with decreased air humidity rarely exceed 24 hours. Variations in growth, therefore, are assumed to be closely correlated to CO_2 assimilation.

The results from Ivantjärnsheden indicate that the varying amounts of CO_2 incorporated in bryophytes during the vegetation period is determined by different climatic variables that replace each other over the year. This agrees with Romose (1940), who presumed that seasonality in length growth of Homalotecium shoots was induced by light or air humidity.

In habitats with heavy litter fall, autumn growth may be inhibited by shading. Rieley et al. (1979) reported from an oak forest in England that no seasonality in the growth of Pleurozium exists.

The two growth maxima assumed for Pleurozium on Ivantjärnsheden is only evident for an exposed habitat in a mature forest in southern Sweden (Figure 9) (Stjernquist 1981). Shoots partly shaded by a tree canopy continue to increase in dry weight during the snow-free months.

Physiological differences between moss species, e.g. different optimum irradiation for photosynthesis and the photosynthetic

capacity of different parts of the shoots, together with the growth form of the moss population, also seem to able to control periodicity. Ptilium crista-castrensis(Hedw.) DNot., like Dicranum growing in tufts, has in both exposed and more shaded habitats continued to grow from March to October with maximum increase in summer (Stjernquist 1981).

To sum up, the discussed growth pattern of the two moss species indicates that no established seasonality exists for coniferous mosses. Instead, the increase in dry weight during the vegetation period varies with habitat and moss species and can be explained by differences in environmental variables, especially irradiation, humidity and litter fall but also concerning internal characteristics, mainly photosynthetic capacity and growth form.

5 REFERENCES

Axelsson, B. and Bråkenhielm, S. 1980. Investigation sites of the Swedish coniferous forest project - Biological and physiographical features. In: Persson, T. (ed.) Structure and Function of Northern Coniferous Forests - An Ecosystem Study. Ecol. Bull. (Stockholm) 32:25-64.

Aronsson, A., Elowson, S. and Ingestad, T. 1977. Elimination of water and mineral nutrition as limiting factors in a young Scots pine stand. I. Experimental design and some preliminary results. Swed.Con.For.Proj.Techn.Rep. 10., pp. 38.

Bates, J.W. 1979. The relationship between physiological vitality and age in shoot segments of Pleurozium schreberi (Brid.) Mitt. J.Bryol. 10:339-351.

Berg, A. 1975. Pigment structure of vascular plants, mosses and lichens at Hardangervidda, Norway. In:Ecol.Stud.17(I):216-224.

Bringmark, L. 1977. A bioelement budget of an old Scots pine forest in central Sweden. Silva Fenn. 11(3):201-209.

Brown, D.H. and Buck, G.W. 1979. Desiccation effects and cation distribution in bryophytes. New Phytol. 82:115-125.

Bråkenhielm, S. and Persson, H. 1980. Vegetation dynamics in developing Scots pine stands in central Sweden. In: Persson, T. (ed.) Structure and Function of Northern Coniferous Forests - An Ecosystem Study. Ecol. Bull. (Stockholm)32: 139-152.

Callaghan, T.V., Collins N.J. & Callaghan, C.H. 1978. Photosynthesis, growth and reproduction of Hylocomium splendens and Polytrichum commune in Swedish Lapland. Oikos 31:73-88.

Dilks, T.J.K. and Proctor, M.C.F. 1974. The pattern of recovery of bryophytes after desiccation. J.Bryol. 8:97-115.

Dilks, T.J.K. and Proctor, M.C.F. 1975. Comparative experiments on temperature responses of bryophytes: Assimilation, respiration and freezing damage. J. Bryol. 8:317-336.

Dilks, T.J.K. and Proctor, M.C.F. 1979. Photosynthesis, respiration and water content in bryophytes. New Phytol. 82:97-114.

Ebeling, F. 1978. Nordsvenska skogstyper. Sver.Skogsvårdsförb. Tidskr. 4:341-381 (In Swedish).

Hagerup, O. 1935. Zur Periodizität im Laubwechsel der Moose. Biol. Medd. K.Dan.Vidensk.Selsk. 11(9), pp. 88.

Hinshiri, H.M. & Proctor, M.C.F. 1971. The effect of desiccation in subsequent assimilation and respiration of the bryophytes Anomodon viticulosus and Porella platyphylla. New Phytol.70: 527-538.

Hoddinott, J. and Bain, J. 1979. The influence of simulated canopy light on the growth of six acrocarpous moss species. Can.J.Bot. 57:1236-1242.

Hoffman, G.R. 1966. Ecological studies of Funaria hygrometrica. Hedw. in eastern Washington and northern Idaho. Ecol. Monogr. 36:157-180.

Ingestad, T. 1967. Methods for uniform optimum fertilization of forest tree plants. In: Proc. 14th IUFRO Congress, Section 22, pp. 265-269.

Kallio, P. and Heinonen, S. 1975. CO_2-exchange and growth of Rhacomitrium lanuginosum and Dicranum elongatum. In: Wielgolaski, E.F. (ed.) Fennoscandian Tundra Ecosystems. I. Plants and Micro-organisms. New York, Springer-Verlag, pp. 138-148.

Kellomäki, S. and Hari, D. 1976. Rate of photosynthesis of some forest mosses as a function of temperature and light intensity and effect of water content of moss cushion on photosynthetic rate. Silva Fenn. 10(4):288-295.

Lackner, L. 1939. Über die Jahresperiodicität in der Entwicklung der Laubmoose. Planta (Berl.) 29:534-616.

Lee, T.E. and La Roi, G.H. 1979.Gradient analysis of bryophytes in Jasper National Park, Alberta. Can.J.Bot. 57:914-925.

Linder, S. 1974. A proposal for the use of standardised methods for chlorophyll determination in ecological and ecophysiological investigations. Physiol. Plant. 32:154-156.

Longton, R.E. and Green, S.W. 1969. The growth and reproductive cycle of Pleurozium schreberi (Brid.)Mitt. Ann.Bot. 33: 83-105.

Longton, R.E. and Green, S.W. 1979. Experimental studies of growth and reproduction in the moss Pleurozium schreberi (Brid.) Mitt. J.Bryol.10:321-338.

Nyholm, E. 1954-69. Musci. In: Illustrated moss flora of Fennoscandia. Ed. The Botanical Society of Lund 2. Lund, Gleerup.

Nörr, M.B. 1974. Drought resistance of mosses. Flora (Jena) 163: 371-387.

Perttu, K., Bishof, W., Grip, H., Jansson, P.-E., Lindgren, Å., Lindroth, A. and Norén, B. 1980. Micrometerology and hydrology of pine forest ecosystems. I. Field studies. In: Persson, T. (ed.) 1980. Structure and Function of Northern coniferous Forests - An Ecosystem Study. Ecol. Bull. (Stockholm) 32:75-121.

Peterson, W.L. and Mayo, J.M. 1975. Moisture stress and its effect on photosynthesis in Dicranum polysetum. Can.J.Bot. 53:2897-2900.

Pitkin, P.H. 1975. Variability and seasonality of the growth of some corticolous pleurocarpous mosses. J.Bryol. 8:337-356.

Rieley, J.O., Richards, P.W. and Bebbington, A.D.L. 1979. The ecological role of bryophytes in a North Wales woodland. J.Ecol. 67:497-527.

Romose, V. 1940. Ökologische Untersuchungen über Homalothecium sericeum, seine Wachumsperioden und seine Stoffproduction, Dan.Bot.Ark. 10:1-134.

Sestak, Z., Catsky, J. and Jarvis, P.G. (ed.) 1971. Plant photosynthetic production. Manual of methods. Dr. W. Junk N.V. Publishers, The Hague, pp. 818.

Shimshi, D. 1969. A rapid field method for measuring photosynthesis with labelled carbon dioxide. J.Exp.Bot. 20:381-401.

Skre, O. and Oechel, W.C. 1979. Moss production in a black spruce Picea mariana forest with permafrost near Fairbanks, Alaska, as compared with two permafrost-free stands. Holarct.Ecol. 2: 249-254.

Stjernquist, I. 1981. Growth and carbon balance of two coniferous forest moss species. Manuscript. Dept. Plant. Ecol. Univ. of Lund.

Stålfelt, M.G. 1937. Der Gasaustausch der Moose. Planta (Berl.) 27:30-60.

Tallis, J.H. 1959. Periodicity of growth in Rhacomitrium lanuginosum. J.Linn.Soc. Lond.Bot. 56(366): 212-224.

Tamm, C.O. 1953. Growth, yield and nutrition in carpets of a forest moss (Hylocomium splendens). Medd. Statens Skogsforskningsinst. 43(1) pp. 140.

Tobiessen, P.L., Slack, N.G. and Mott, K.A. 1979. Carbon balance in relation to drying in four epithytic mosses growing in different vertical ranges. Can.J.Bot. 57:1994-1998.

Watson, M. 1975. Annual periodicity of incremental growth in the moss Polytrichum commune. Bryologist 78:414-422.

ACKNOWLEDGEMENTS

I want to express my gratitude to Prof. N. Malmer, Dept. of Plant Ecology, University of Lund, for valuable advice and discussions. I would also like to thank the following persons for helpful support and criticism: G. Hansson, J. Hellkvist, K. Hillerdal-Hagströmmer, H. Staaf, S. Söderlund and M. Varga.

Table 1.

Occurrence and appearance of the dominant species in the bottom layers at IhV (120-year-old stand) and Ih II (20-year-old stand). Ih II is exposed to different amounts of water and nutrients.

Stand treatment	PLEUROZIUM SCHREBERI		DICRANUM POLYSETUM	
	occurrence	appearance	occurrence	appearance
Ih V	dominant	growing in loose mats, developed lateral branches	patchily distributed in pure carpets	erect shoots growing in tufts
Ih II, Control	patchily distributed in the neighbourhood of vegetation	developed lateral branches	patchily distributed in small tufts	erect shoots growing in tufts, head-like shoots
Ih II, Irrigation	dominant	growing in loose mats, developed lateral branches	patchily distributed in pure carpets	erect shoots, growing in tufts
Ih II, Irrigation + Fertilization	common	erect shoots growing in dense tufts, almost no lateral branches, thin shoots	common, pure carpets	erect shoots growing in dense tufts, thin shoots

Table 2. Climatic data for sampling days during growth seasons 1976 and 1977

Date	Type of weather	Max. irradiance (µE)	Variation in temperature (°C)	Variation in relative air humidity (% RH)
1976-07-06	Varying cloudiness	1850	6 - 20	100 - 33
1976-07-07	Clear, some cloudiness at midday	1850	7 - 21	100 - 36
1976-08-25	Clear, rain at 21 h.	1620	5 - 20	100 - 42
1976-08-26	Rain until noon, thereafter clear weather	1650	10 - 16	100 - 60
1976-08-27	Cloudy	1250	3 - 16	100 - 70
1977-07-12	Clear until about 11 h., thereafter cloudy. Clear weather in evening	1660	4 - 20	89 - 35
1977-07-13	Cloudy	400	3 - 12	85 - 57
1977-08-16	Varying cloudiness	1200	7 - 23	94 - 46
1977-08-17		1500(40)*	4 - 22(11-20)*	100 - 40(100-65)*
1977-08-18	Clear until about 08 h., thereafter cloudy. Light rain from about 16 h.	1100	6 - 16	100 - 74
1977-11-10	Clear weather	350	(-3)-(+8)	100 - 66

* Exposed area (shaded area)

Table 3.

Analyses of variance illustrating the partial relationship between assimilation rate of Pleurozium and Dicranum (dependent variables) and climatic variables (independent variables) as well as the effect of shading. The material from morning (a.m.) and afternoon (p.m.) periods were analysed separately.

*** = p <0.001, ** = p <0.01, * = p <0.05, n.s. = not significant.

PLEUROZIUM	a.m. (n=45)	p.m. (n=25)
Variable	F-ratio	F-ratio
Irradiance	37.85 ***	19.92 ***
Temperature	5.23 *	2.10 n.s.
VPD	5.00 *	22.02 ***
Category		
Shading	2.12 n.s.	17.65 ***
Variance explained	61%	56%

DICRANUM	a.m. (n=45)	p.m. (n=24)
Variable	F-ratio	F-ratio
Irradiance	30.99 ***	23.90 ***
Temperature	0.26 n.s.	3.85 n.s.
VPD	0.21 n.s.	13.76 ***
Category		
Shading	1.80 n.s.	16.63 ***
Variance explained	70%	68%

Table 4.

Rank of independent variables and multiple correlation coefficient from a stepwise linear regression analysis applied to the relation between assimilation rate of Pleurozium and Dicranum (dependent variables) and climatic variables (independent variables). n.s. = not significant.

	Rank	Variable	Multiple corr. (r)	Significance of inclusion (p)
PLEUROZIUM	1	VPD	0.37	<0.01
	2	Irradiance	0.57	<0.001
	3	Temperature	0.57	n.s.
DICRANUM	1	Irradiance	0.57	<0.001
	2	VPD	0.69	<0.001
	3	Temperature	0.70	n.s.

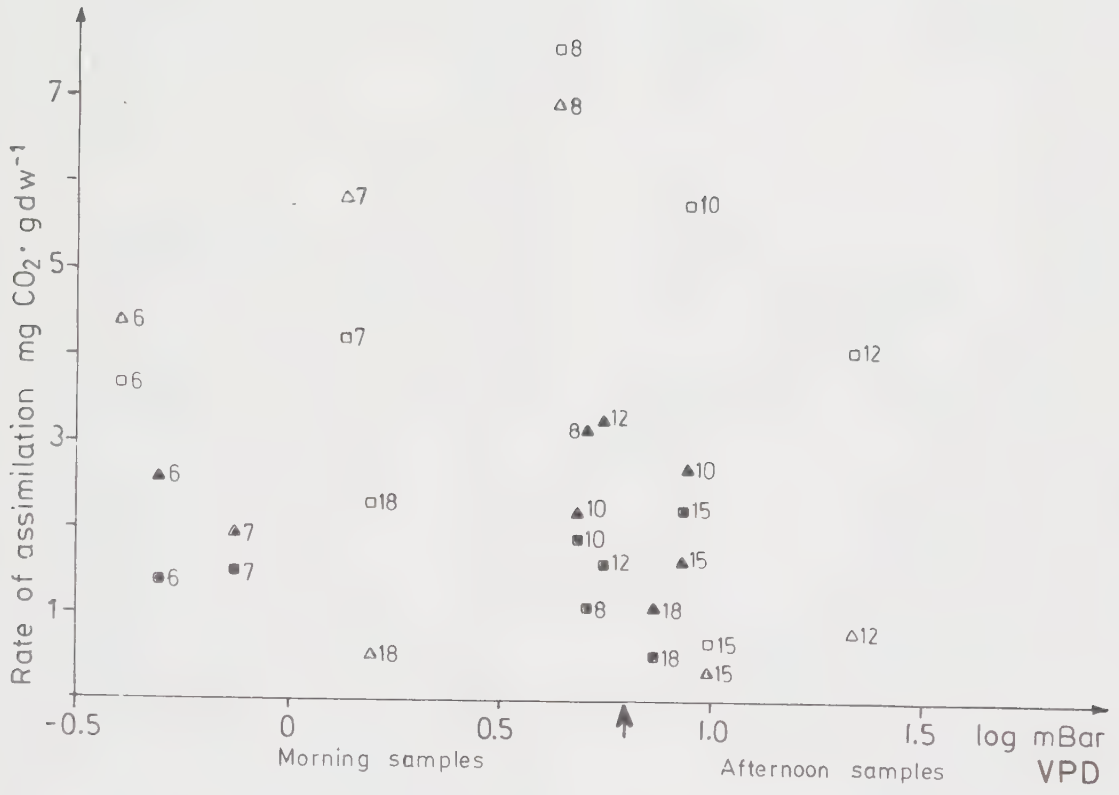


Figure 1. The relationship between assimilation rate of Pleurozium schreberi and Dicranum polysetum and air humidity on Ih II:IF, exposed (light symbols) and shaded (dark symbols) habitat, in August 1977. Symbols: Pleurozium △ , Dicranum □ .

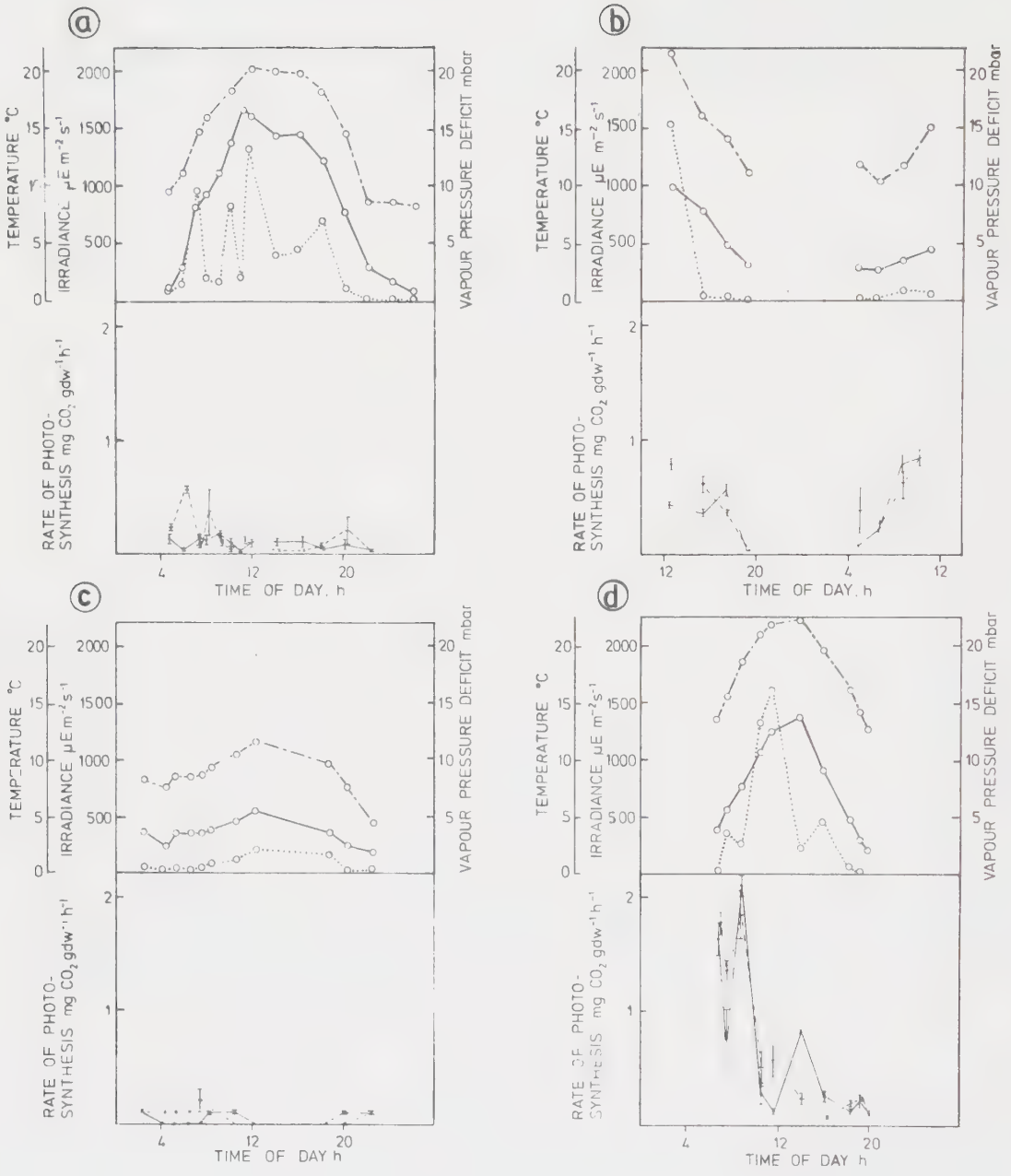


Figure 2.Climatic conditions and gross photosynthetic rate of Pleurozium schreberi and Dicranum polysetum at IhV on four sampling occasions. a. July 6,1976. b.August 26-27,1976. c.July 13,1977. d.August 16,1977. Symbols: Pleurozium ———, Dicranum - - - - -, photon flux density ...., air temperature -.-.-.- and air humidity o———o

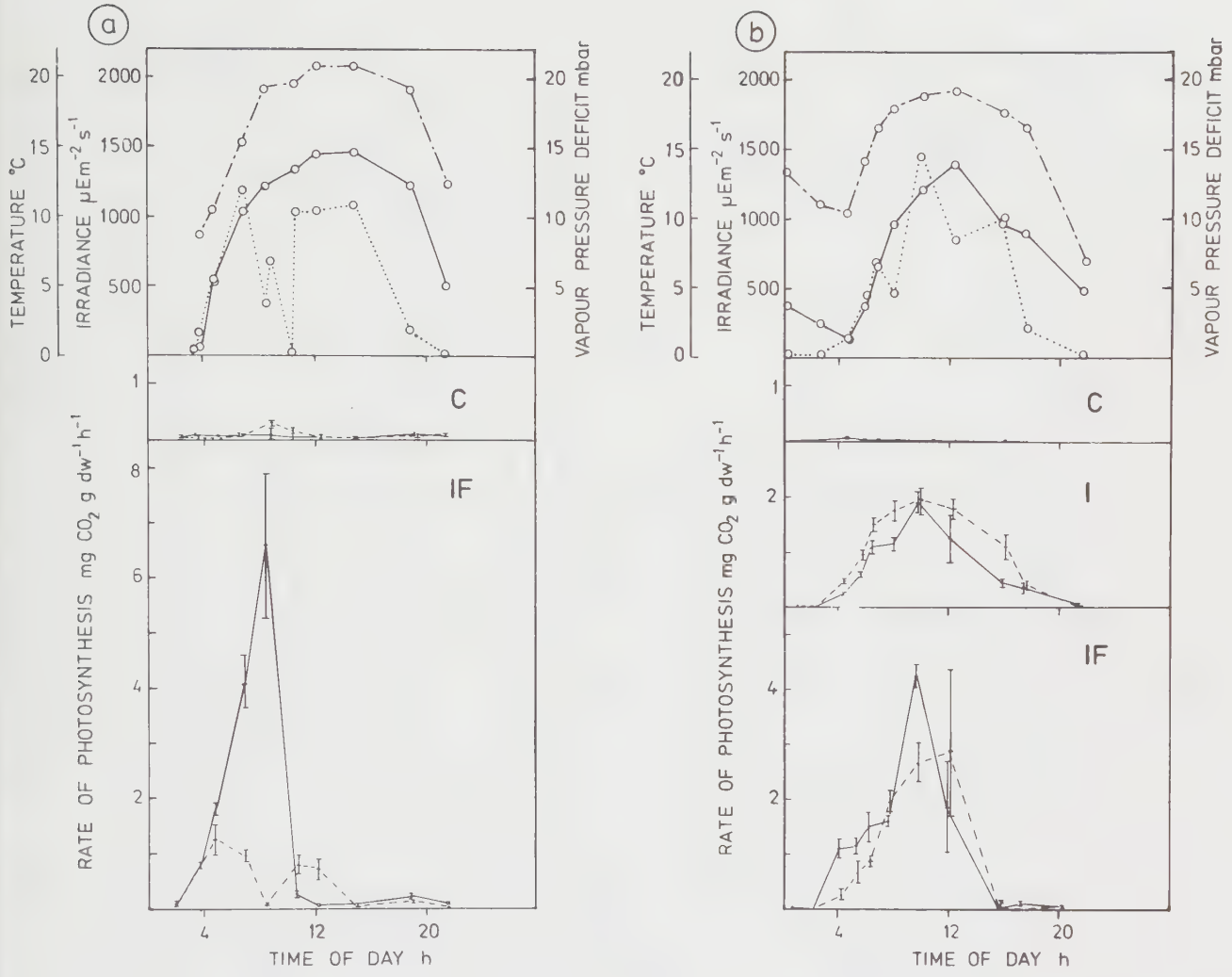


Figure 3. Climatic conditions and gross photosynthetic rate of Pleurozium schreberi and Dicranum polysetum at Ih II:C,I,IF. a. July 7,1976. b. July 12,1977. Symbols: Pleurozium ———, Dicranum - - - -, photon flux density ....., air temperature -.-.-, and air humidity o———o.

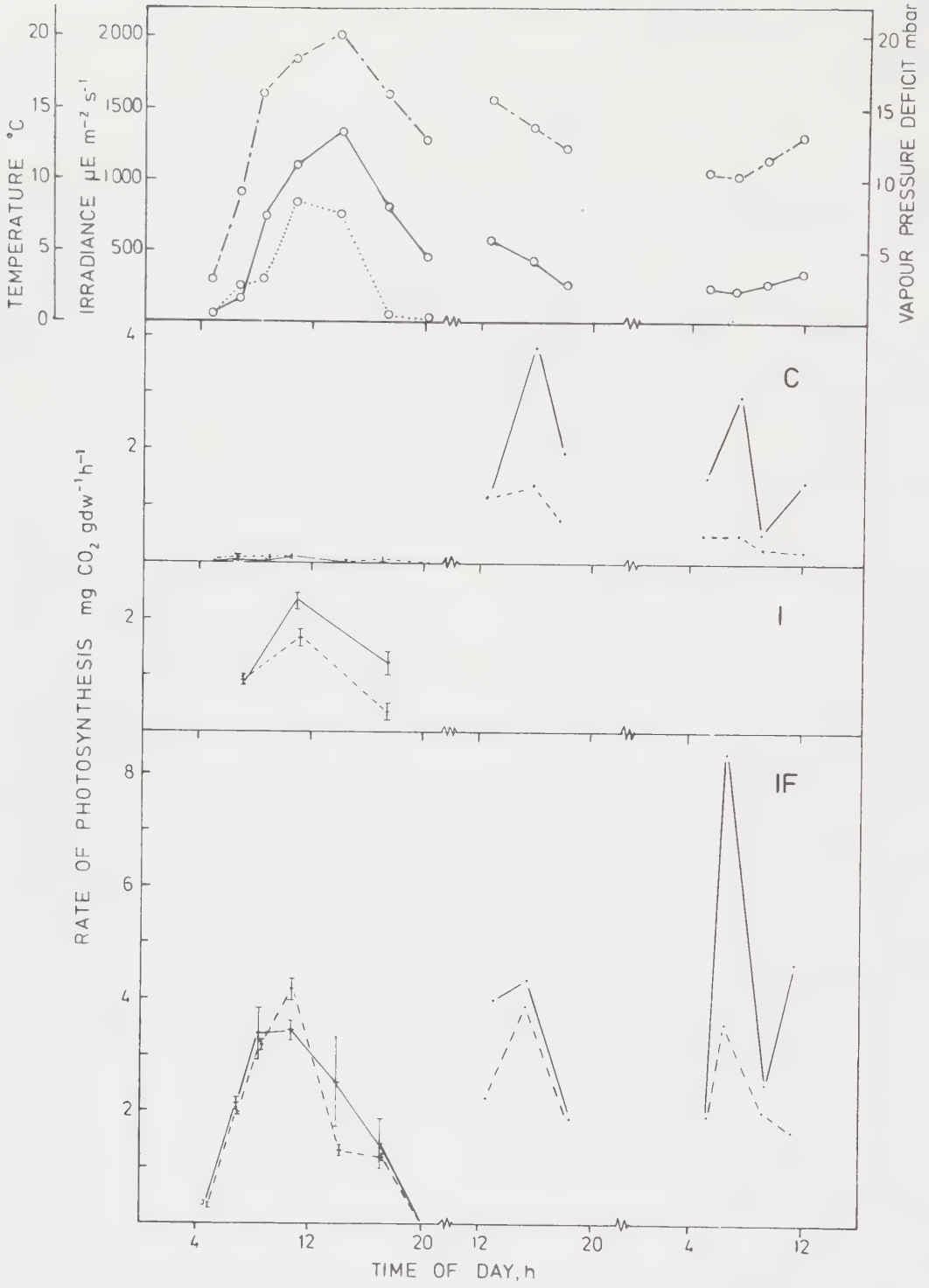


Figure 4. Climatic conditions and gross photosynthetic rate of Pleurozium schreberi and Dicranum polysetum at Ih II:C,I,IF during August 25-27,1976.
Symbols: Pleurozium ————, Dicranum - - - -, photon flux density ....., air temperature -.-.- and air humidity o————o.

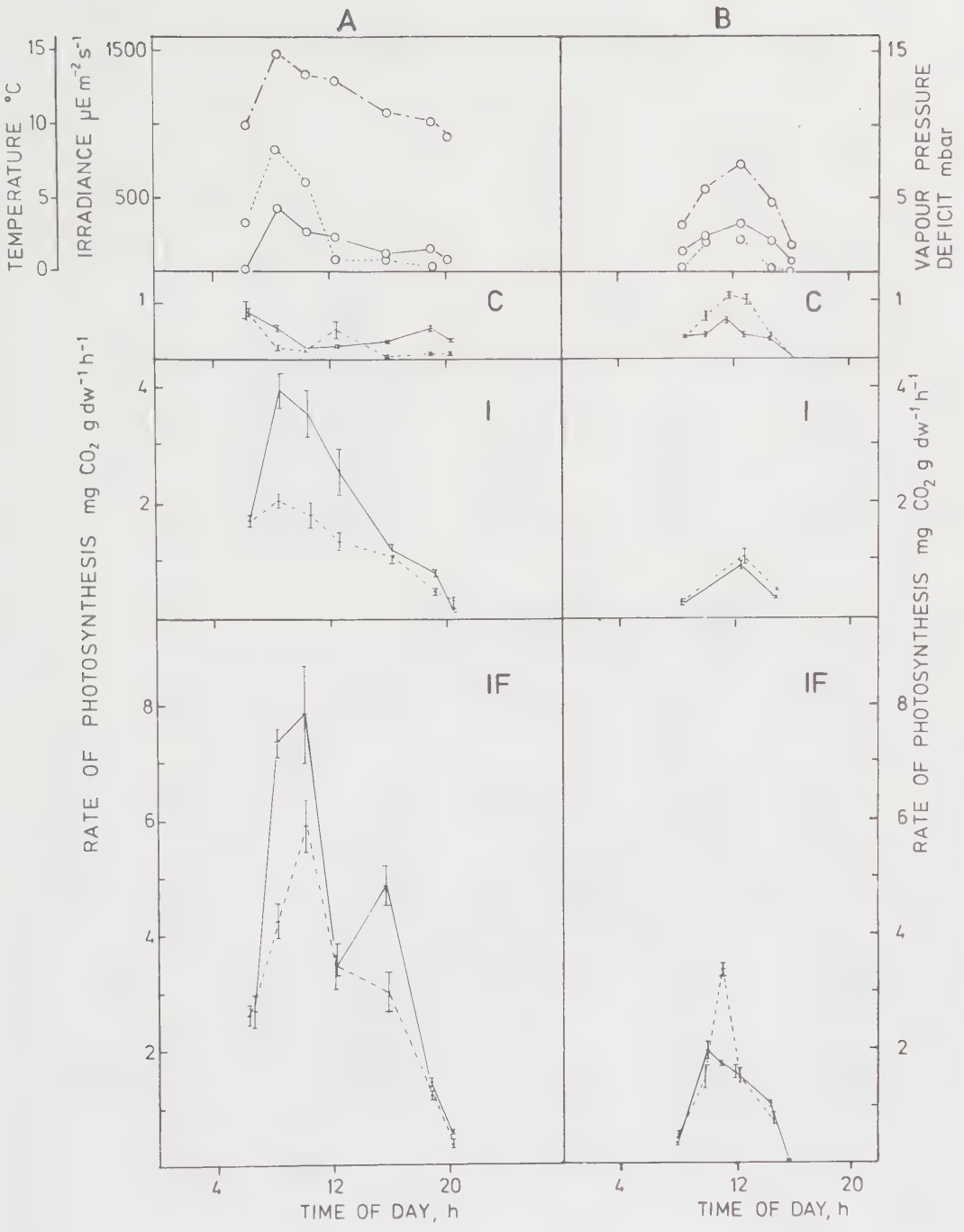


Figure 5.Climatic conditions and gross photosynthetic rate of Pleurozium schreberi and Dicranum polysetum at Ih II:C,I,IF. a. August 18,1977. b. November 10,1977. Symbols: Pleurozium ————, Dicranum - - - -, photon flux density ....., air temperature -.-.-.- and air humidity o————o.

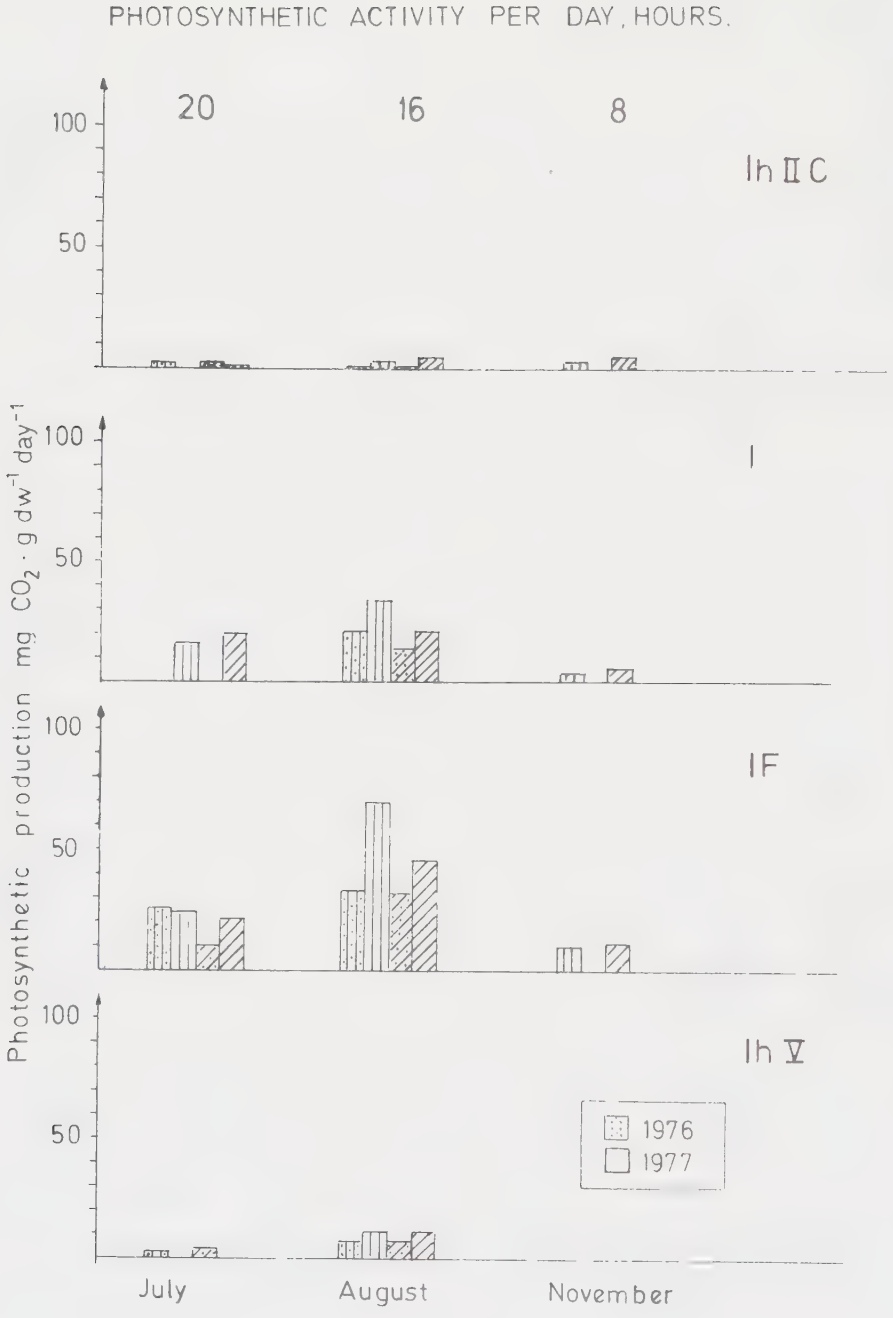


Figure 6. The diurnal CO_2 fixation and the number of hours with photosynthetic activity at Ivantjärnsheden (Ih II:C,I,IF; IhV) in July,August and November 1976 and 1977.

Symbols: Pleurozium schreberi
Dicranum polysetum

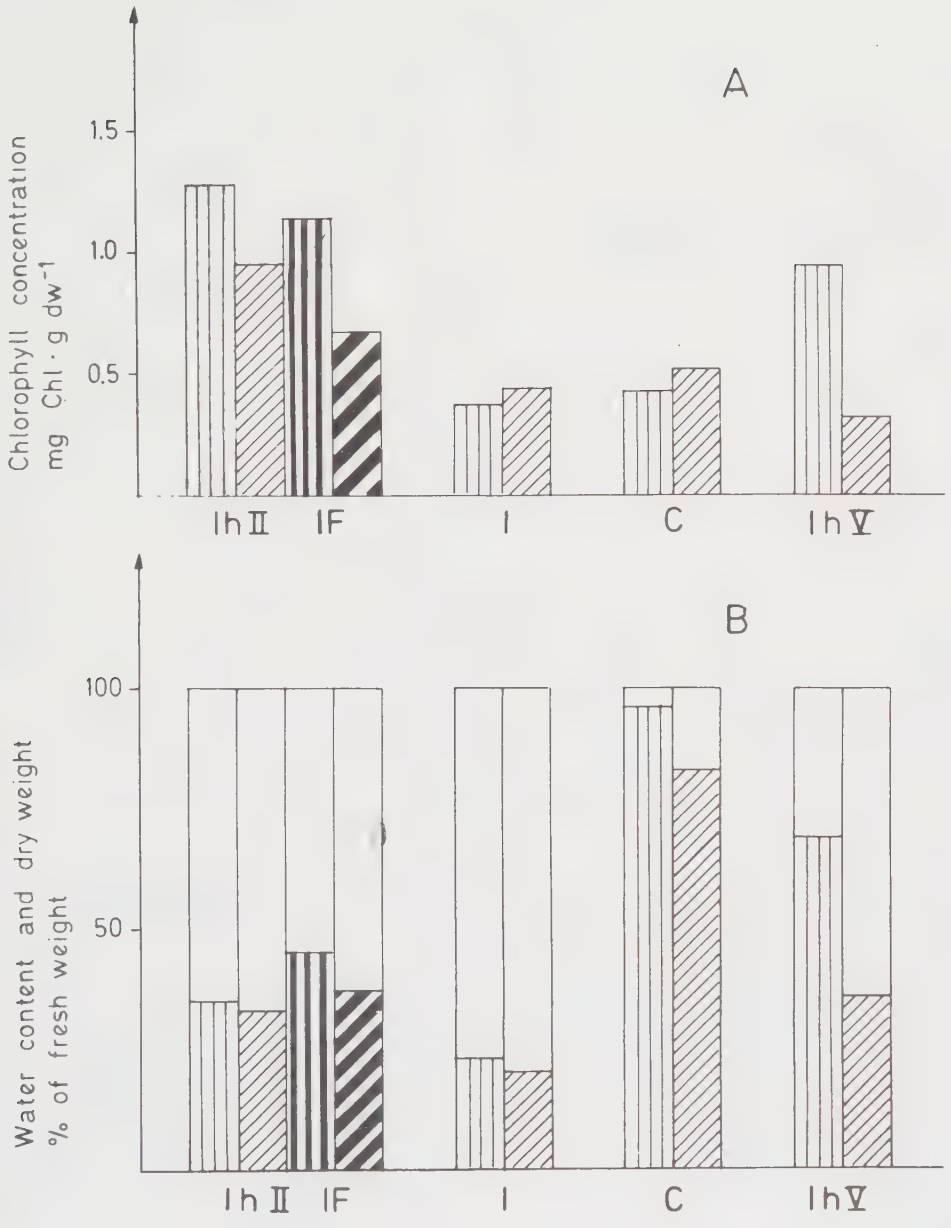


Figure 7a. Chlorophyll concentration in Pleurozium schreberi and Dicranum polysetum at Ivantjärnsheden (Ih II:C, I, IF; IhV) in August 1977.

Symbols: Pleurozium exposed site ▥, shaded site ▥
Dicranum " " ▨ " " ▨

7b. Water content and dry weight of Pleurozium schreberi and Dicranum polysetum at Ivantjärnsheden (Ih II:C, I, IF; IhV) in August 1977. Symbols as above.

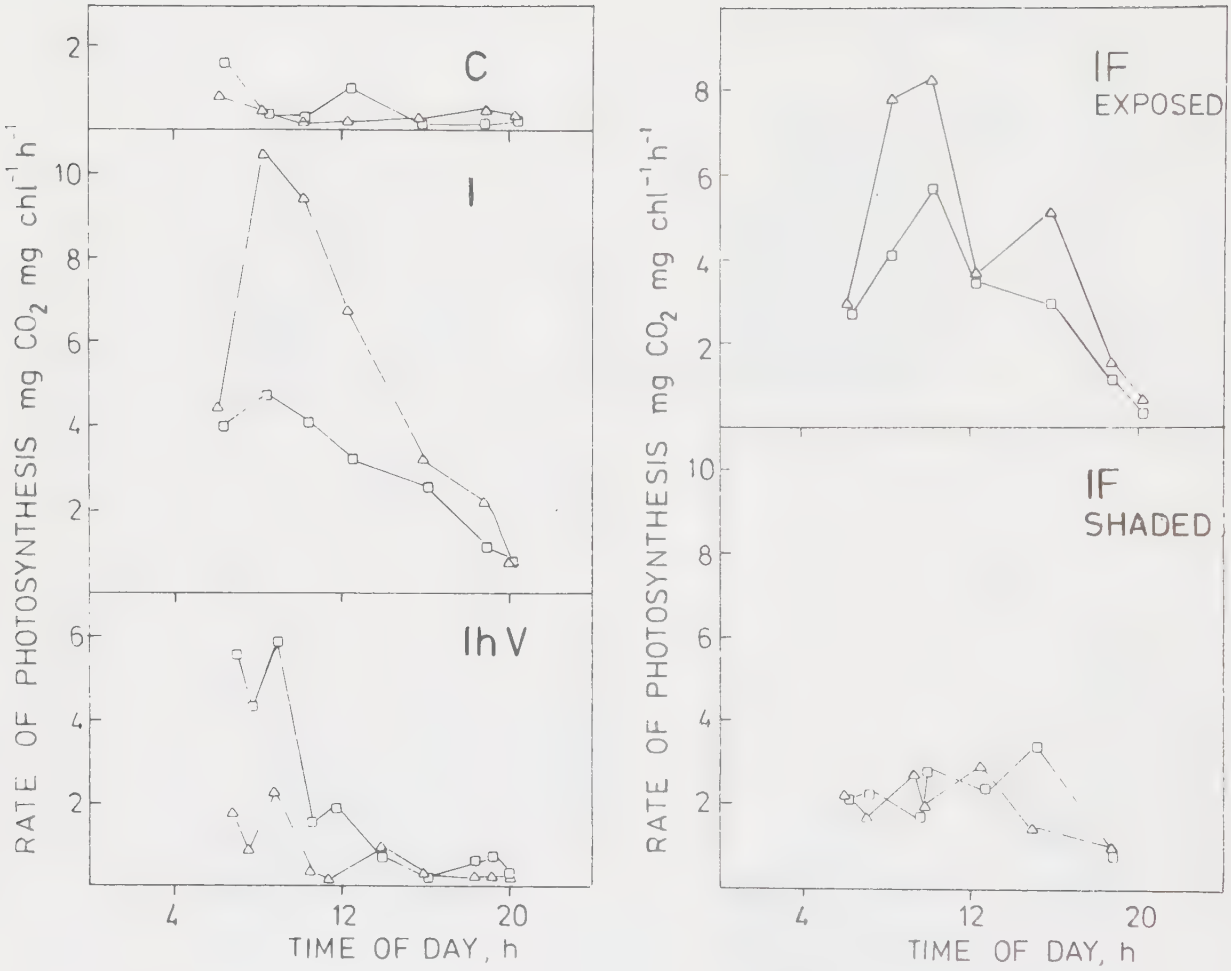


Figure 8. Gross photosynthesis rate per mg chlorophyll of Pleurozium schreberi and Dicranum polysetum at Ivantjärnsheden (Ih II:C,I,IF; IhV) in August 1977. Symbols: Pleurozium △ , Dicranum □ .

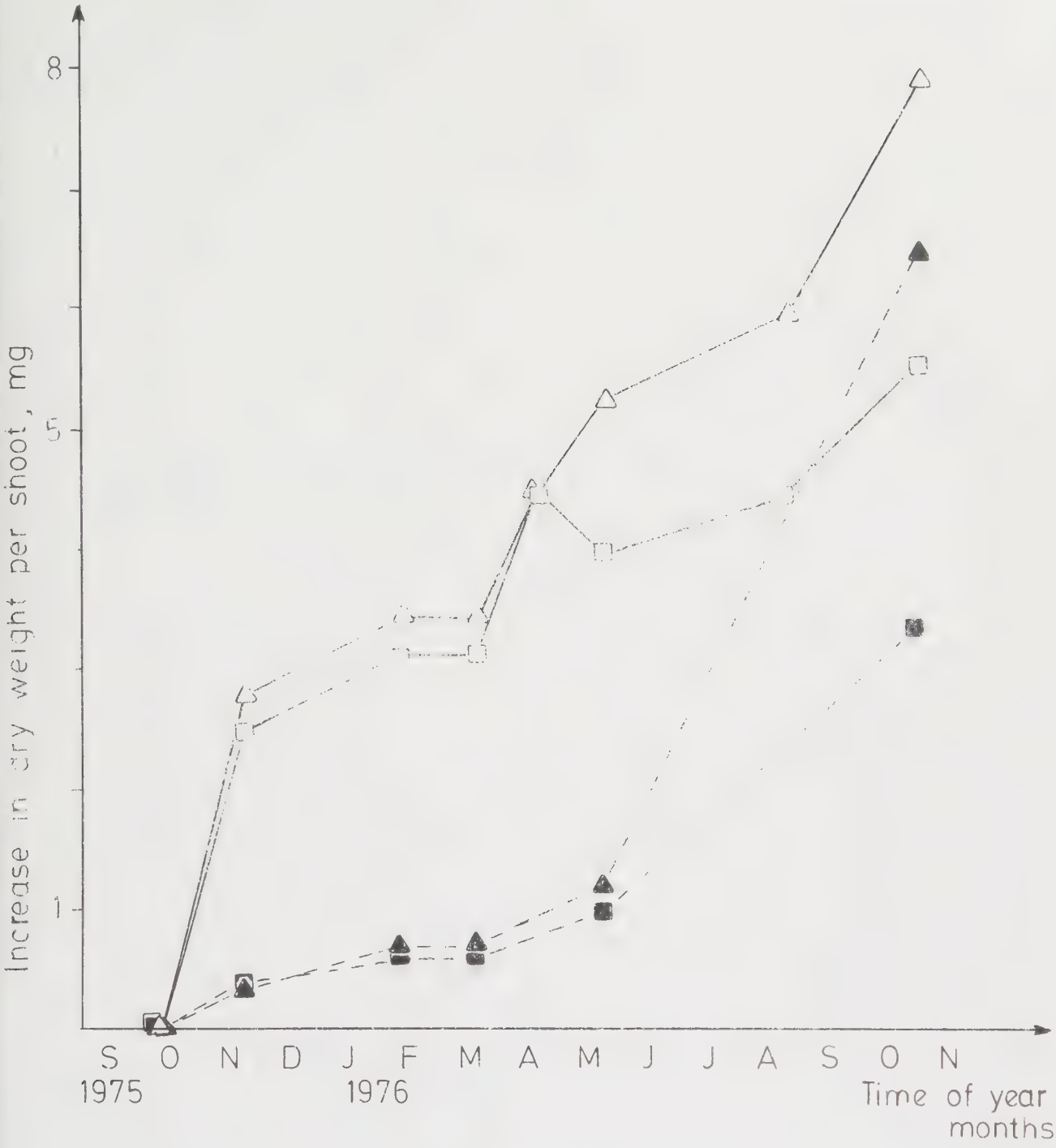


Figure 9. Increase in dry weight of Pleurozium schreberi and Ptilium crista-castrensis in a mature spruce-pine forest at Nyteboda 1976.
Symbols: Pleurozium: dry habitat △——△, moist habitat □——□. Dicranum: dry habitat ▲- - -▲, moist habitat ■- - - -■.

GROWTH AND CARBON BALANCE OF TWO CONIFEROUS FOREST MOSS SPECIES

Ingrid Stjernquist

Department of Plant Ecology
Helgonavägen 5
S-223 62 LUND
Sweden

ABSTRACT

Variations in growth of Pleurozium schreberi (Brid.). Mitt. and Ptilium crista-castrensis (Hedw.) DNot. were studied during a year in five experimental plots, placed beneath a spruce (1 and 2), at the canopy border (3) and in a glade (4 and 5), and representing different micro-climatic conditions of a mature coniferous forest in Southern Sweden. The diurnal CO_2-assimilations of three days, representative for spring, summer and autumn climate, were also determined. Parallel measurements of climatic variables and litterfall were also made.

For both moss species, maximum growth took place in the most humid habitat, plot No. 5, and decreased in the order of 5-3-4--1-2 for Pleurozium and 5-4-3-1-2 for Ptilium. Pleurozium had the highest annual increase in dry weight but the growth fluctuated between periods and habitats. The maximum value was measured in September-November on plot 5 with 2.8 mg·shoot^{-1}, and the minimum in April on plot 4 with -0.5 mg·shoot^{-1}. Growth of Ptilium was constantly less, with a maximum in May-October on plots 3-5. No seasonal pattern was discernible beneath the spruce canopy.

When the two bryophytes were compared the assimilation rate of Ptilium was significantly higher at low light intensities, 15-80 $\mu E\ m^{-2}s^{-1}$ and at reduced humidity, 70% RH.

On the Pleurozium and Ptilium shoots, 4 cm and 3 cm respectively were photosynthetically active with maximum CO_2-fixation 1-2 cm from the apex. The carbon content of the "illuminated" and the remaining "green" part of the Pleurozium shoot was higher than that of Ptilium. Of the "attached dead" fraction, 23% had decomposed after two years on plots 3-5. No decomposition could be found on plots 1-2.

It is assumed that three factors regulate growth of Pleurozium and Ptilium: The maximum assimilation capacity of different segments of the shoot, growth form and the reaction to micro-climate conditions. The effects of the investigated environmental variables on the competitive ability of the bryophytes in the five habitats are discussed.

1 INTRODUCTION

In mature coniferous forests the bottom layer gives an important contribution to the dry matter production of the ecosystem. Mälkönen (1974) has calculated it to be 10-20% of the above-ground tree production in a Finnish pine forest. The frequent bryophytes belong to a few species, forming wide, more or less pure carpets. With only few exceptions, these moss species have no internal water conduction (cf. Tansley and Chick 1901, Bayfield 1973) and the production is therefore more directly dependent on climatic factors than that of vascular plants.

Single climatic variables and their effect on photosynthesis of coniferous bryophytes have been studied by several authors, especially irradiation and temperature (cf. Stålfelt 1937, Tamm 1953, Hicklenton and Oechel 1976, 1977, Källomäki and Hari 1976, Oechel 1977) , humidity and desiccation (cf. Klepper 1963, Dilks and Proctor 1974, 1975, Peterson and Mayo 1975). The influence of irradiation, temperature and desiccation seems to be dependent on species and to some extent independent on each other. On the other hand, from a general point of view, high humidity is required for maximum photosynthesis.

Morphological factors seem to be of importance in differentiating photosynthetic activity between moss species. Krupa (1978), for example, has demonstrated the relationship between leaf area structure and photosynthesis at constant irradiation.

However, bryophytes with low sexual and asexual reproduction and with similar life strategy, like the coniferous forest moss species, may largely depend on production as a means of competition (cf. During 1979). Annual production of the moss carpet has been determined to 43 $g \cdot m^{-2}$ in a dry 120-year-old Swedish Scots pine forest (Persson 1980). Values 3-4 times higher, 120 $g \cdot m^{-2}$, have been reported for spruce forests in Finland (Källomäki *et al.* 1977) and in Alaska 150-180 $g.m^{-2}$ (Skre and Oechel 1979). Tamm (1953) gives the moss production in several coniferous forests in Norway and Sweden, falling in the range

25-140 $g.m^{-2}$, and also demonstrates that the variation within the forest is greater than between the experimental sites.

Watson (1980) found that along a altitudinal gradient, the distribution of Polytrichum species is dependent on the microhabitat. The distribution of a specific moss species within an ecosystem may in a similar way be related to the micro-climate via its influence on the productivity of the shoots. The production achieved might therefore be influenced by three regulating factors: The assimilation potential, the growth form and the micro-climate.

Moss species visually co-existing in the bottom layer of a coniferous forest may have different occurrences in nature. Pleurozium schreberi, thus, is a widespread bryophyte also common in open areas, on heaths and in mountains. In contrast, the species with the smallest amplitude, Ptilium crista-castrensis, very seldom grows outside the forest (Nyholm 1954-69). The two mosses belong to the same family and both have pinnate shoots with small concave leaves, but Pleurozium grows in loose mats and Ptilium in tufts. A bryophyte often occurring intertwined with Pleurozium is Dicranum polysetum. This species has the same growth form as Ptilium but the shoots have large,spreading leaves, most frequent at the top. In an earlier investigation it was found that the climate variable mainly controlling the assimilation capacity of Dicranum seems to be irradiation. Compared to Pleurozium, the bryophyte probably has a higher competitive ability in darker and drier habitats (Stjernquist 1981).

The aims of this paper were: (a) to study whether morphological and environmental factors regulate the photosynthesis of Pleurozium schreberi and Ptilium crista-castrensis, (b) if so, to study whether the in situ growth during the year and the carbon balance depend on variations of these factors, and (c) to analyse the competitive ability of the moss species in different micro-habitats, representative of a coniferous forest.

2 MATERIAL AND METHODS

2.1 Site description

The investigation site chosen was a 200-year-old coniferous forest in the southern part of Sweden, 35 km north of Kristianstad ($56^{o}20'N$, $14^{o}23'E$). The site is a nature preserve with no silvicultural impacts. The forest consists of a tree layer, dominated by Norway spruce Picea abies Karst. and a bottom layer of Pleurozium schreberi (Brid.) Mitt., Ptilium crista-castrensis (Hedw.) DNot. and Dicranum polysetum Sw. Five experimental plots, Nos. 1-5, were placed along a gradient from a spruce trunk into a glade, to represent five different micro-climatic conditions typical of the forest (Fig. 1). Two of the plots (1 and 2) were placed under the spruce canopy, No. 1 close to the trunk. Plot No. 3, situated at the canopy border, was the one most affected by throughfall from the tree. Plot No. 4 was exposed to high irradiation, especially in summer. A small swamp near plot No. 5 presented more humid conditions than the others in the gradient.

2.2 Field experiment

The investigation period lasted from September 1975 to October 1976. Tufts of Pleurozium and Ptilium respectively were randomly collected on two reference sites, each of 10 x 10 metres. From this sampling moss shoots were randomly chosen, cut to a length of 4.0 cm and planted in circular plots of 1 m^2, already containing the experimental species. The plots were divided into 8 sectors and 30 shoots of each species were planted one by one in rows with 2 cm intervals. Each individual experimental shoot replaced a naturally growing moss shoot, and therefore the density of the moss carpet in each plot was the same as before the start of the experiment. Determinations of weight and length of transplanted shoots were made six times for Pleurozium and four times for Ptilium during the investigation period. Thirty shoots of each moss species were sampled per plot and sampling occasion.

During three days in May, June and October respectively - chosen to be representative of average climatic conditions of spring, summer and autumn - the assimilation rates of Pleurozium and Ptilium were determined as $^{14}CO_2$-incorporation according to Shimshi (1969) at intervals of 1-3 hours. For further discussion of the method, see Hillerdal-Hagströmmer and Stjernquist (1980). On each investigation occasion five parallel measurements were made. The diurnal gross photosynthesis was estimated by interpolation between the measurement points and integrating of the area under the assimilation graphs obtained. Temperature, relative humidity and irradiation were studied in parallel with the thermohygrograph (Lambrecht) and quantasensor (Lambda, 400-700 nm) respectively.

Biomasses of the "chlorophyll-containing" part and "attached dead" of pure stands of Pleurozium and Ptilium were estimated in June. Within frames of 1 dm^2 ten samples of each species were punched and the number of shoots and the dry weight determined (85°C, 24 hours). The "chlorophyll-containing" part was assumed to comprise the distance from the apex to the point where the green colours vanished and was divided into an "illuminated" and a "green" part. The average dry weight of a shoot of 4 cm was estimated from 100 individuals and the annual growth calculated as the sum of the periodical increase in dry weight. The"illuminated"part was determined in the laboratory from 30 individuals as the average length in mm directly reached by light from a lamp vertically fixed above an intact moss carpet.

For Pleurozium the decomposition rate at the five experimental plots was investigated using the litter bag technique for three consecutive periods during two years. The litter bags were constructed from nylon web with 1 mm mesh size, and the original dry weights were approximately the same, about 0.5 g.

Litter fall from the tree canopy was registered during summer and winter 1976 with five litter traps, each with an area of 1 dm^2, placed along the gradient. In the laboratory the litter from each trap was spread over an area of the same size, and the decrease in irradiation caused by the litter layer was

determined with a quantasensor at 730 μE $m^{-2}s^{-1}$ and 430 μE $m^{-2}s^{-1}$.

2.3 Laboratory experiments

Eighty randomly collected shoots of Pleurozium, Ptilium and Dicranum from the reference sites at Nyteboda were cut in sections of 1.0 cm and placed in plexiglass cuvettes with constant climate (irradiation 430 μE · $m^{-2}s^{-1}$, relative humidity 100% and temperature 15°C). Each cuvette contained 40 shoots placed with the same density as at the reference site. The net photosynthesis rate of the different moss sections was estimated using gas exchange technique, CO_2 being detected with an infra-red analyser (URAS 2). At the end of the experiment the mosses were dried for 24 hours at 85°C and weighed.

Four batches of 40 shoots each of Pleurozium and Ptilium were prepared. Two were allowed to grow in a constant relative humidity of 70% with 12 hours´ day and 12 hours´ night, and two were exposed to varying conditions of humidity during a day, 2 hours´ 20% RH, 2 hours´ 100% RH and 20 hours´ 70% RH divided in two periods. After a week the mosses were remoistened and changes in the net photosynthetic ability with time were examined with the same method as described above.

2.4 Statistical treatment

In a separate study the standard deviation of photosynthetic rate measured in different cuvettes, each containing 40 shoots at optimal climatic conditions, was estimated to be 11% of the mean value (N=9) (Stjernquist and Ingelög 1981).

The differences in growth between vegetation periods were tested for significance with the t-test. Differences between Pleurozium and Ptilium concerning biomass and length of shoot segments were tested with the same method.

3 RESULTS

3.1 Growth and biomass increase

The total accumulation of organic matter through growth was less for Ptilium than for Pleurozium in all the five experimental plots (Table 1a, b). With the exception of the most exposed site, this also applied to the increase in length (Table 1c). Maximum growth took place in plot No. 5 and decreased in the order of 5-3-4-1-2 for Pleurozium and 5-4-3-1-2 for Ptilium. The large confidence interval of the figures from sites under the spruce canopy was due to the fact that only some of the investigated shoots of both moss species showed any increase in length and weight. The averages of the total sampling number in plot No. 1 were 75% for Ptilium and 66% for Pleurozium and in plot No. 2, 62% and 49% respectively. The existing new Pleurozium shoots were dark green and very thin.

The relative order of increase in biomass of differently exposed plots changed during the vegetation period. Outside the tree canopy, Ptilium had the highest growth from May to October. In early spring shoots at the canopy border were the most favoured. Under the canopy the increase in weight throughout the year had no discernible seasonal pattern.

The growth of Pleurozium showed a more varying pattern than that for Ptilium. On the most exposed growth site, plot No. 4, accumulation of organic matter fluctuated from a maximum in September to November to negative value in April. With the exception of the winter period, biomass increments on plot No. 5 fluctuated similarly to those of No. 4, but the oscillations were more moderate. At the canopy border the highest Pleurozium production was in early spring and from August to October. For shoots growing beneath the spruce, the increase in biomass was low but reached a maximum in August to October.

3.2 Carbon assimilation

The assimilation rate of Pleurozium and Ptilium on the same experimental plots and the relationship between the plots along the gradient varied throughout the year (Fig. 2 a-c). Late in autumn, with high relative humidity and a temperature of 2-7°C, the CO_2 incorporation of the two species was small, especially under the tree canopy. At this time of the year the most exposed plot showed the highest assimilation rate.

The day selected in the spring, like the one in the autumn, had good humidity conditions and a temperature around 10°C, but irradiation was 5 times higher at noon, which stimulated photosynthesis and increased assimilation by 20-100 times.

The summer study consisted of two extremely contrasting climatic conditions. The afternoon of June 17 was the last part of a warm and dry period and the assimilation rate was near zero for both moss species. A rainfall gave optimum humidity during the second part of the study, but the irradiation decreased to the level of the spring day. Assimilation was, however, constantly lower in all habitats. Mosses at the canopy border had a decreased photosynthetic ability in summer and spring compared to plots Nos. 4 and 5.

The comparison between the two moss species shows that the assimilation rate of Ptilium was more stimulated at low light intensity than that of Pleurozium. In autumn, for instance, when irradiation was 15 $\mu E,m^{-2}s^{-1}$, the CO_2-incorporation was twice that of Pleurozium. In spring, Ptilium on the dark plots, i.e. Nos. 1 and 2 (maximum 25 $\mu E,m^{-2}s^{-1}$), still photosynthesized more than Pleurozium, but at 80 $\mu E,m^{-2}s^{-1}$ the assimilation rates were equal.

Measurements of the CO_2-exchange under controlled conditions in the laboratory indicated that long, dry periods with constant relative humidity of 70% negatively affected net photosynthesis but did not completely kill the moss shoots of Pleurozium and Ptilium (Fig. 3). After rewetting, the respiration losses

continued at least for one hour after treatment. Pleurozium was the most sensitive species with negligible photosynthesis after 27 hours. A short period with 100% RH per day was enough for quick recovery after rewetting, even if the bryophytes were exposed to 20% RH for about 2 hours. The hours with high air humidity also caused maximum photosynthesis that, after the recovering period for both mosses, was significantly higher ($p<0.01$) than the CO_2-exchange after continuous drought. Nevertheless, Pleurozium had a greater respiration loss and significantly ($p<0.05$) lower net photosynthesis after 27 hours than Ptilium.

3.3 Structure and activity of the moss carpet

The length and dry weight of the "chlorophyll-containing" and "illuminated" part of a Ptilium moss carpet was significantly smaller compared to that of Pleurozium (Table 3). Four cm of the Pleurozium and 3 cm of the Ptilium shoots had positive net photosynthesis with maximum assimilation between 1-2 cm from the apex (Fig. 4). However, Dicranum, the third dominant bryophyte of the bottom layer, had maximum assimilation in the uppermost centimetre of the shoot.

Pleurozium on the reference site had significantly higher carbon content per unit ground area for the "illuminated" part, $p<0.05$, and the "attached dead", $p<0.01$ (Figure 5). Plot No. 5 closely corresponds to the reference site and the values were assumed to be representative for that habitat. The length of the "attached dead" segment was estimated to be twice the annual shoot length, provided that decomposition rates of the moss species were low enough for the stems to remain intact for two years. Together with the measured "chlorophyll-containing" part of the shoot measured in June, this would result in a carpet thickness of 7.4 cm for Pleurozium and 6.1 cm for Ptilium. Only the "green" segment of a Ptilium shoot was estimated to be longer than the corresponding segment of Pleurozium.

3.4 Litter fall

In winter, the decrease in irradiation reaching the bottom layer depending on litter fall was greatest near the spruce stem, 71%, and at a minimum, 24%, in the glade. In summer, however, litter fall was heavier at the canopy border (Table 4).

3.5 Decomposition

The biomass fraction transferred to "attached dead" decomposed slowly in all experimental plots (Table 5). After two years, the maximum loss was 23% of original weight and visually this lost part only consisted of the leaves. Only stems and branches were left, which are likely to remain for a long time in the humus layer. No decomposition could be noted under the spruce canopy and the small increase in dry weight of the litter bags was probably due to an input of spruce needles and other litter components. Decomposition ceased in all plots in summer, as hardly any weight losses were noted during the period July-September. Even during spring the decomposition was very small.

4 DISCUSSION

4.1 Growth-regulating factors

Three factors have hypothetically been assumed to regulate the growth of Pleurozium and Ptilium. The first is the maximum assimilation capacity of different segments of the living moss shoot, which probably are of fundamental importance for the resulting production of the species. Bryophytes with distinct annual shoots, e.g. Hylocomium splendens, seem to have a biomass development mainly restricted to a short period of the year and therefore show a stepwise decrease of net photosynthesis with increasing age (Callaghan et al. 1978, Skre and Oechel 1979). On the other hand, Pitkin (1975), measuring shoot elongation of epiphytic bryophytes in deciduous forests in England, found a continuous growth over the year. In most habitats Pleurozium and Ptilium, representing the mosses of the forest floor with no periodic morphological development of the shoots, increase in dry weight during any period without snow cover (Table 1, Fig. 2). Bates (1979) reported that when Pleurozium shoots were divided into segments of 2 cm the CO_2-exchange decreased with distance from the apex. The two mosses and the third dominating species in the investigated forest, Dicranum, show two different patterns of assimilation activity. Pleurozium and Ptilium have their maximum photosynthetic rate 1-2 cm from the apex, whereas the top cm of Dicranum is responsible for 50% of the total CO_2 fixation per shoot. The assimilation potential of a moss shoot may probably be the same during the year but the continuous growth means that for a specific segment the assimilation capacity will change as the shoot grows further.

In spite of the similar patterns of assimilation capacity in the shoots of Pleurozium and Ptilium, the maximum increase in dry weight differs in time between the species. Pleurozium has the highest growth in autumn and Ptilium in summer. Growth form and morphology of the bryophytes is the second growth-regulating factor which modifies the ability of a certain moss species to utilize maximum net assimilation of different parts of the shoots.

Pleurozium growing in loose mats seems to be able to take advantage of the most active segment down to 3 cm from the apex (Table 3). Dicranum and Ptilium, however, both grow in tufts (Nyholm 1954-69). The photosynthetic ability of Dicranum may only be slightly reduced by the growth form (cf. Stjernquist 1981). Ptilium, with 52% of the "chlorophyll-containing" shoot illuminated, probably encounters a decreased irradiation caused by self-shading already in the potentially most active section. The growth pattern may negatively influence the assimilation rate, especially during periods with low irradiation. Because such a situation often occurs during the autumn period, when water conditions are at optimum for photosynthesis, the increase in dry weight of Ptilium during this period will be low compared to Pleurozium. The greatest growth on the exposed plot of the gradient in September to November also supports the assumption that Ptilium shoots in many places are unable to utilize their photosynthetic capacity to a maximum. Sites with heavy litter fall strengthen the effect of self-shading. Differences in morphology and growth form of the moss species also determine the share of the moss shoot illuminated and as a consequence the thickness of living biomass in the bottom layer.

The importance of the third regulating factor is shown by the five experimental plots at Nyteboda representing five different micro-climatic situations typical of a spruce forest in a late successional stage. The number of days without snow cover, especially at the end of March, seemed to determine growth during the winter months. Plot No. 3 had the shortest snow period of the glade sites and plot No. 5 the longest. Under favourable water conditions Ptilium has a higher assimilation rate at decreased irradiation than Pleurozium (Fig. 2a, c). Further, Ptilium may be less sensitive to continuous low relative humidity and to very low humidity during a short period during a day as long as the relative humidity at night reaches 100%. Growing in tufts the shoots may also be able to decrease the desiccation rate by maintaining humidity around the moss shoots (Peterson

and Mayo 1975). This probably allows Ptilium to utilize short moist periods more efficiently than Pleurozium, thus enabling photosynthesis to start earlier and reach a higher value after a long drought (Fig. 2b). The growth form of Ptilium extends the photosynthetic period of the day compared to species growing in mats or loose tufts. Such properties may to some extent compensate for the negative influence of self-shading on the in situ photosynthesis.

If the gross production during 24 hours is adjusted with respect to dark respiration and the three factors discussed above, the resulting net production seems to closely correspond to the carbon accumulation in situ (Table 2). Only the periods just before and after snow cover have been chosen for the comparison with the assumption that rainfall and decreased evaporation in late autumn and the melting snow in spring provide water conditions that do not restrict photosynthesis and respiration. The period is also estimated to consist of days with minimum CO_2-assimilation (diurnal assimilation measured in October) from November to snow cover at the end of January and days with maximum assimilation in April (diurnal assimilation measured in May) (Fig. 2a, c). Only days with a temperature over $0^{\circ}C$ and a minimum of 80% RH are included. A temperature of $10^{\circ}C$ caused a diurnal respiration loss of 2.4 mg C per g dw for Pleurozium and 2.3 mg C per g dw for Ptilium. A temperature of $2^{\circ}C$ decreased respiration loss to 7.0 and 17.0 µg C per dw and day respectively. Respiration under the snow cover with temperatures of $0^{\circ}C$ and lower is assumed to be insignificant (cf. Stålfelt 1937, Dilks and Proctor 1975). The climatic influence on moss production also embraces a decrease in irradiation because of varying amounts of litter fall to the bottom layer at different habitats. The difference between the production of Pleurozium on plot No. 1 as measured with the two methods probably depends on unfavourable moisture conditions in situ. The large standard deviation for increase in length and dry weight on the plot indicates that the figure may also be influenced by differences in the number of growing shoots and the relationship between weight and length. The low production of Ptilium in the most exposed

habitat may be an effect of desiccation at the beginning of the period. For Pleurozium this effect is hidden by the high production in early spring.

The increase in length at different periods during the year will determine the transformation of living tissue to "attached dead", if the "illuminated" part is constant. In all sites outside the tree canopy the increase in shoot length for both Pleurozium and Ptilium is most pronounced in June to November and therefore causes maximum formation of dead biomass during this period. The decomposition rate is insignificant in summer, giving no carbon loss until autumn and the following spring. Moss species with hard stems and branches, e.g. Pleurozium, probably decompose in two stages. In moist habitat with maximum decomposition, all the leaves have disappeared after two years but the stems, which contain about 80% of the initial dry weight, may be preserved unaffected in the humus layer for a longer time. Transformation of biomass to "attached dead" under a tree canopy may be more complicated because of the irregular growth and the large amount of litter fall. Probably, some cells all over the shoot gradually die off, as occurs in Pleurozium in total darkness (Stjernquist and Ingelög 1981).

4.2 Habitat differentiation and moss growth

The influence of climatic factors on photosynthesis and growth of Pleurozium and Ptilium, as found in laboratory experiments and earlier investigations (cf. Källomäki and Hari 1976, Källomäki et al. 1977), was supported by the in situ production of different micro habitats in the spruce ecosystem (Table 1). In moist habitats (e.g., plot No. 5), Pleurozium has a continuous growth. This corresponds to the results of Tallis (1959) for the moss Rhacomitrium lanuginosum in humid climate. The increase in dry weight of the shoots in every experimental period is higher compared to other habitats. The lower value in April compared to plots Nos. 3 and 4 may be explained by a longer period with snow cover in winter (Table 2).

Pleurozium often grows in open and exposed habitats without a protective tree canopy, corresponding to plots 3 and 4, in spite of the decrease in growth by desiccation. Dry periods, especially in spring when humidity at night is lower than 100%, even stops photosynthesis, resulting in a net carbon loss in the moss. The ability to survive in such environment may probably be determined by the autumn production and the number of days with optimum humidity and high irradiation just after snow cover.

Tamm (1964) and Longton & Green (1979) assumed that higher concentrations of essential nutrient substances in the precipitation at the canopy border stimulated the growth of coniferous bryophytes. Fertilization experiments with Pleurozium and Dicranum have shown a positive correlation between growth and nutrient concentration (cf. Stjernquist 1981). If the nutrient concentration is one factor regulating moss production in situ, growth at the canopy border (plot No. 3) will increase compared to an open field with the same irradiation conditions. For Pleurozium this situation only exists in August to mid-October and in April. At the same time, litter fall from the canopy decreases irradiation to the bottom layer considerably more than in the glade. Later in autumn when irradiation is low (Fig. 2c), shading from the heavy litter fall makes it impossible for the bryophytes to take advantage of higher nutrient concentration.

Habitats under a dense tree canopy contain no or very few moss species. In the investigation sites at Nyteboda, Dicranum species are the only bryophytes naturally growing on plot No. 1. The decrease of irradiation and humidity caused by the tree does not seem to inhibit the assimilation rate of Pleurozium enough to explain the absence of the species (Fig. 2). The increase in dry weight, especially in late summer, probably is satisfactory for the survival of the species, but a low number of growing shoots and a variation in growth with many long and very thin shoots, indicate that the situation is unfavourable to the species. Hoffman (1966) observed that with reduced irradiation intensity, shoots of Funaria hygrometrica become taller and

thinner. Such growth of the new shoot section might be caused by the fact that the dense litter fall may cut off the segment with maximum photosynthesis.

The capacity of Ptilium to withstand decreased relative humidity and the more complex photosynthetic reactions to irradiation, with counteracting factors involved, results in a small but similar growth in habitats outside the tree canopy during the greatest part of the snow-free period. The differences in total annual growth between the habitats, which nevertheless exist, are probably due to differences in desiccation during a rather short period in late summer and early autumn, when there is still sufficient irradiation for maximum photosynthesis in the second segment of the moss shoots. In contrast to Pleurozium, the growth of Ptilium will not be stimulated by higher irradiation, e.g. in summer and in exposed habitats in- and outside the forest. Because of the dense tufts and erect shoots, dark periods, especially in late autumn, and dark habitats only produce a small increase in dry weight. The normal morphology of the annual shoots at decreased irradiation indicates, however, that it may be possible for Ptilium to survive in dark places for extended periods of time.

Habitats with heavy litter fall dramatically reduce growth. Litter from broad-leaved species will be more shading to the bottom layer than needle litter, which often sinks down in the moss carpet between the shoots. This phenomenon may be an important reason why Ptilium nearly exclusively appears in coniferous forests of a late successional stage (Nyholm 1954-69, Slack 1977).

The negative effect of litter fall seems to offset possible growth stimulation depending on increased nutrient concentration in the throughfall at the canopy border. Like Pleurozium the large growth at the beginning of May may be determined by the early melting of the snow cover as compared to the other habitats outside the canopy.

4.3 Species distribution

Moss species coexisting at equilibrium may have similar photosynthetic reactions to environmental variables but still occupy separate niches. Schuster (1957), Levin (1970) and Slack (1977) have, however, assumed that bryophytes forming large, pure patches in a habitat have had a competitive advantage in time over other species invading the place. The distribution of the three dominant moss species in Nyteboda therefore probably reflects the combined long-term effect on production and carbon distribution of the growth factors discussed above. The optimum climatic conditions for both Pleurozium and Ptilium are found in humid places with moderate irradiation. If the increases in dry weight of the two species are compared, Pleurozium seems to be superior in every kind of habitat examined. The bryophyte has significantly higher carbon incorporation of a single shoot, but because of the greater amount of shoots per dm^2 for Ptilium, this difference disappears on an area basis. The significantly higher living biomass estimated for pure Pleurozium tufts may indicate growth of older segments, probably as increase of branches and the formation of new lateral shoots. The number of new lateral shoots will be of importance when the bryophyte gets the opportunity to increase its distribution.

What factors make it possible for Ptilium to break the superiority of Pleurozium in certain habitats? A slight tendency towards faster growth in length in exposed habitats (No. 4) may in time give Ptilium the advantage by shading, provided that litter fall is moderate. Even if the annual difference in length between the species is not quite significant, the ability of Ptilium to withstand desiccation causes a continuous increase in length and dry weight for this bryophyte during spring and summer. This displacement in time of maximum growth probably makes it possible for Ptilium to decrease irradiation to levels further down in the moss carpet. Because Pleurozium has a high irradiation demand for maximum photosynthesis and has the photosynthetically most active part 1-2 cm from the apex, the shading effect may change the competitive ability to the advantage of Ptilium. In dark habitats

however, two factors positive for Ptilium may cooperate. Firstly, the low optimum irradiation value of Ptilium will result in higher photosynthesis compared to Pleurozium. Secondly, the energy reserve of Pleurozium may probably be concentrated in the long, thin and dark green annual shoots. If these shoots do not reach more favourable irradiation conditions, the growth potential of Pleurozium will be reduced.

Dicranum, the third dominant species on the forest floor, resembles Ptilium because the CO_2-fixation seems to remain high in dark or dry habitats. The bryophyte is often found in pure carpets beneath a closed tree canopy. One factor of importance for the difference in distribution between Dicranum and Ptilium within a mature coniferous forest seems to be the greater ability of Dicranum to withstand the effects of litter fall, on account of the top cm being responsible for at least 50% of the total amount of organic matter produced by a shoot. When the needles sink down into the moss carpet, the head of the Dicranum shoots will be exposed to almost the same light intensity which reaches the bottom layer. In contrast, this upper part of Ptilium only accounts for 30% of the production and therefore the shading effect of the litter may be more negative for the growth of Ptilium.

5 REFERENCES

Bates, J.W. 1979. The relationship between physiological vitality and age in shoot segments of Pleurozium schreberi (Brid.) Mitt. J.Bryol. 10:339-351.

Bayfield, N.G. 1973. Notes on water relations of Polytrichum commune Hedw. J. Bryol. 7:607-617.

Callaghan, T.V., Collins, N.J. and Callaghan, C.H. 1978. Photosynthesis, growth and reproduction of Hylocomium splendens and Polytrichum commune in Swedish Lapland. Oikos 31:73-88.

Dilks, T.J.K. and Proctor, M.C.F. 1974. The pattern of recovery of bryophytes after desiccation. J. Bryol. 8:97-115.

Dilks, T.J.K. and Proctor, M.C.F. 1975. Comparative experiments on temperature responses of bryophytes: Assimilation, respiration and freezing damage. J. Bryol. 8:317-336.

During, H.J. 1979. Life strategies of bryophytes: A preliminary review. Lindbergia 5:2-18.

Hicklenton, P.R. and Oechel, W.C. 1976. Physiological aspects of the ecology of Dicranum fuscescens in the subarctic I. Acclimation and acclimation potential of CO_2-exchange in relation to habitat, light and temperature. Can.J.Bot.54: 1104-1119.

Hicklenton, P.R. and Oechel, W.C. 1977. The influence of light intensity and temperature on the field carbon dioxide exchange of Dicranum fuscescens in the subarctic. Arct.Alp. Res. 9(4):407-419.

Hillerdal-Hagströmmer, K. and Stjernquist, I. 1980. Rate of photosynthesis in dominating species in tree-, field- and bottom layers of an old and a young stand of Scots pine at varying water and nutrient status. Swed.Con.For. Proj.Int. Rep. 96, pp. 44 (In Swedish).

Hoffman, G.R. 1966. Ecological studies of Funaria hygrometrica Hedw. in eastern Washington and northern Idaho. Ecol. Monogr. 36:157-180.

Klepper, B. 1963. Water relations of Dicranum scoparium. Bryologist 66:41-54.

Krupa, J. 1978. Phytosynthesis rate in moss leaves of various anatomical structure. Acta Soc.Bot.Polonia 47:391-402.

Källomäki, S. and Hari, P. 1976. Rate of photosynthesis of some forest mosses as a function of temperature and light intensity and effect of water content of moss cushion on photosynthetic rate. Silva Fenn. 10(4):288-295.

Källomäki, S., Hari, P. and Wäisänen, E. 1977. Annual production of some forest mosses as a function of light available for photosynthesis. Silva Fenn. 11(1):81-86.

Levin, S. 1970. Community equilibria and stability and an extension of the competitive exclusion principle. Am.Nat. 104:413-420.

Longton, R.E. and Green, S.W. 1979. Experimental studies of growth and reproduction in the moss Pleurozium schreberi (Brid.) Mitt. J.Bryol. 10:321-338.

Mälkönen, E. 1974. Annual primary production and nutrient cycle in some Scots pine stands. Commun.Inst.For.Fenn. 84.(5),pp.87.

Nyholm, E. 1954-69. Musci In: Illustrated Mossflora of Fennoscandia. Ed. The Botanical Society of Lund. 2. Lund, Gleerup.

Oechel, W.C. 1976. Seasonal patterns of temperature response of CO_2 flux and acclimation in arctic mosses growing in situ. Photosynthetica (Prague) 10(4):447-456.

Persson, H. 1980. Structural properties of the field and bottom layers at Ivantjärnsheden. In Persson T. (ed.) Structure and Function of Northern Coniferous Forests - An Ecosystem Study. Ecol. Bull. (Stockholm) 32:153-163.

Peterson, W.L. and Mayo, J.M. 1975. Moisture stress and its effect on photosynthesis in Dicranum polysetum. Can.J.Bot. 53:2897-2900.

Pitkin, P.H. 1975. Variability and seasonality of the growth of some corticolous pleurocarpous mosses. J.Bryol. 8:336-356.

Schuster, R.M. 1957. Boreal Hepaticae, a manual of the liverworts of Minnesota and adjacent regions II. Ecology. Amer. Midl.Nat. 57:203-299.

Shimshi, D. 1969. A rapid field method for measuring photosynthesis with labelled carbon dioxide. J.Exp.Bot. 20:381-401.

Skre, O. and Oechel, W.C. 1979. Moss production in a black spruce Picea mariana forest with permafrost near Fairbanks, Alaska, as compared with two permafrost-free stands. Holarct.Ecol. 2:249-254.

Slack, N. 1977. Species, diversity and community structure in bryophytes: New York State studies. N.Y. State Mus. Bull. 428, pp. 70.

Stjernquist, I. 1981. The influence of nutrient and climatic variables on the field CO_2 assimilation of Pleurozium schreberi and Dicranum polysetum and their effect on seasonality of growth. Manuscript. Dept. Plant Ecol. Univ. of Lund.

Stjernquist, I. and Ingelög, T. 1981. Effects of silvicultural herbicides on the photosynthesis of seven bryophyte species. Manuscript. Dept. Plant Ecol. Univ. of Lund.

Stålfelt, M.G. 1937. Der Gasaustausch der Moose. Planta(Berl.)25: 30-60.

Tallis, J.H. 1959. Studies in the biology and ecology of Rhacomitrium lanuginosum Brid. II. Growth reproduction and physiology. J.Ecol. 47:325-350.

Tamm, C.O. 1953. Growth, yield and nutrition in carpets of a forest moss (Hylocomium splendens). Medd.Statens Skogsforskningsinst. 43(1) pp. 140.

Tamm, C.O. 1964. Growth of Hylocomium splendens in relation to tree canopy. Bryologist 67:423-426.

Tansley, A.G. & Chick, E. 1901. Notes on conducting tissue-system in Bryophyta. Ann.Bot. (Lond.) 15:1-41.

Watson, M.A. 1980. Shifts in patterns of microhabitat occupation by six closely related species of mosses along a complex altitudinal gradient. Oecologia (Berl.) 47:46-55.

ACKNOWLEDGEMENTS

I want to express my gratitude to Prof. N. Malmer and Prof. M. Sonesson, Dept. of Plant Ecology, University of Lund, for valuable advice and discussions. I would also like to thank the following persons for helpful support and critisism: G. Hansson, I. Nilsson, M. Sillén, H. Staaf, S. Söderlund and M. Varga.

Table 1a.

Growth of Pleurozium schreberi, expressed as mg dry weight per shoot. Mean values and their 95% confidence limits and the significance of the biomass change during each period are also given (N=30).

* = P<0.05; ** = P<0.01; *** = P<0.001; ns = not significant.

Growth period	Days	Plot No. 5	4	3	2	1
26/09-07/11	41	2.79±0.56 ***	2.49±0.50 ***	1.39±0.52 ***	-0.09±0.16 ns	0.36±0.89 ns
07/11-02/04	*)	1.74±0.89 ***	2.01±0.77 ***	2.31±1.27 ***	0.24±0.26 ns	-0.34±0.32 ns
02/04-07/05	35	0.81±1.11 ns	-0.50±1.08 ns	0.50±1.74 ns	-	-
02/04-10/06	68	-	-	-	0.24±0.39 ns	0.74±0.33 ***
07/05-06/08	87(5-3)	0.68±0.27 ***	0.48±0.15 ***	0.21±0.11 ***	-	-
10/06-06/08	56(1-2)	-	-	-	-0.01±0.10 ns	0.08±0.07 *
06/08-13/10	67	1.93±0.63 ***	1.12±0.62 ***	1.94±0.83 ***	0.25±0.20 ns	0.28±0.17 **
1 year		7.46	5.32	5.86	0.56	1.05

* See Table 2.

le 1b.

wth of Ptilium crista-castrensis, expressed as mg dry weight per shoot. Mean values and their 95% fidence limits and the significance of the biomass change during each period are also given (n=30). p<0.05; ** = p<0.01; *** = p<0.001; ns = not significant.

wth iod	Days	Plot No. 5	4	3	2	1
09-07/11	41	0.34±0.11 ***	0.38±0.11 ***	0.24±0.10 ***	0.06±0.04 **	0.03±0.03 *
11-04/03	*)	0.33±0.21 **	0.19±0.16 *	0.19±0.17 *	0.04±0.07 ns	0.16±0.07 ***
03-07/05	63	0.51±0.26 **	0.48±0.25 ***	0.61±0.24 ***	0.19±0.11 **	0.11±0.10 *
05-13/10	156	5.29±1.31 ***	2.34±0.40 ***	1.71±0.97 ***	0.21±0.19 *	0.44±0.22 ***
ear		5.89	3.14	2.56	0.48	0.70

See Table 2.

le 1c.

wth of Pleurozium schreberi and Ptilium crista-castrensis from 1975-09-26 to 1976-10-13, expressed as er shoot. Mean values and their 95% confidence limits and the significance of differences between cies are given (n=30).

cies	Plot No. 5	4	3	2	1
rozium	17.2±7.6	10.8±6.9	12.6±6.3	3.6±3.8	5.6±5.2
	p<0.1	ns	p<0.01	ns	ns
lium	14.3±4.2	13.7±8.3	9.3±2.9	3.7±3.5	4.9±3.8

Table 2.

Growth of Pleurozium schreberi and Ptilium crista-castrensis as estimated from gas exchange data and weight analyses, expressed as mg incorporated C per shoot. Growth periods: 75-11-07--76-04-02 and 75-11-07--76-03-04 respectively.

Plot No.	5	4	3	2	1
PLEUROZIUM					
Gas exchange	0.79	1.01	1.03	0.11	0.02
Weight analyses	0.78	0.90	1.04	0.11	-0.15
Days with max + min photosynthesis	5+76	6+76	9+76	8.5+91.5	5+86
PTILIUM					
Gas exchange	0.11	0.22	0.09	0.02	0.01
Weight analyses	0.15	0.09	0.09	0.02	0.07
Days with max + min photosynthesis	0+76	0+76	0+76	0+91.5	0+86

Table 3.

"Illuminated"(a) and "chlorophyll"-containing part (b) of shoots from two moss species. Mean value and standard deviations are given (n=30).

	a		b	
	mm	mg dw	mm	mg dw
Pleurozium schreberi	29 ± 3	10.4	40 ± 5	14.4 ± 5.0
Ptilium crista-castrensis	17 ± 2	5.4	33 ± 5	10.4 ± 3.5

Table 4.

Decrease of irradiation reaching the bottom layer on account of litter fall, expressed as per cent of total irradiation.

	Plot No.				
	5	4	3	2	1
Winter 75-10-22--76-03-26	24	24	40	58	71
Summer 76-03-26--76-09-18	-	27	44	20	32

Table 5.

Decomposition losses of Pleurozium schreberi in the five experimental plots, expressed as per cent of original weight. The experiment started 17 Jan. 1975.

Sampling date	Incubation period (days)	Plot No. 5	4	3	2	1
1975-07-02	166	5	4	5	1	3
1975-09-17	77	5	4	3	+1	+1
1977-03-25	797	23	14	11	+8	+7

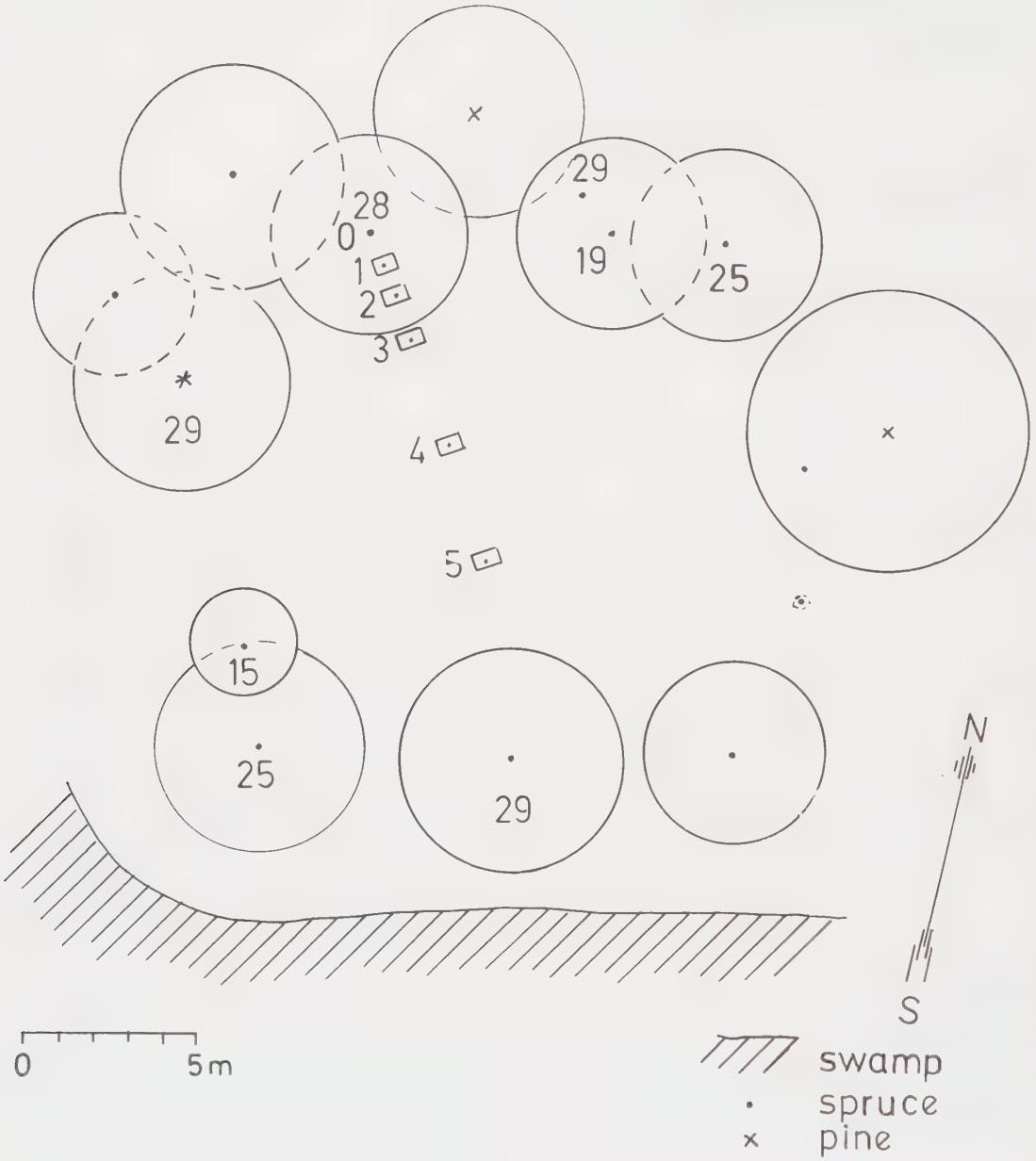


Figure 1. The experimental layout at Nyteboda research area. The numbers indicate the position of the investigation plots according to the surrounding trees. The figure at each stem gives the height of the tree and the circles show the canopy area.

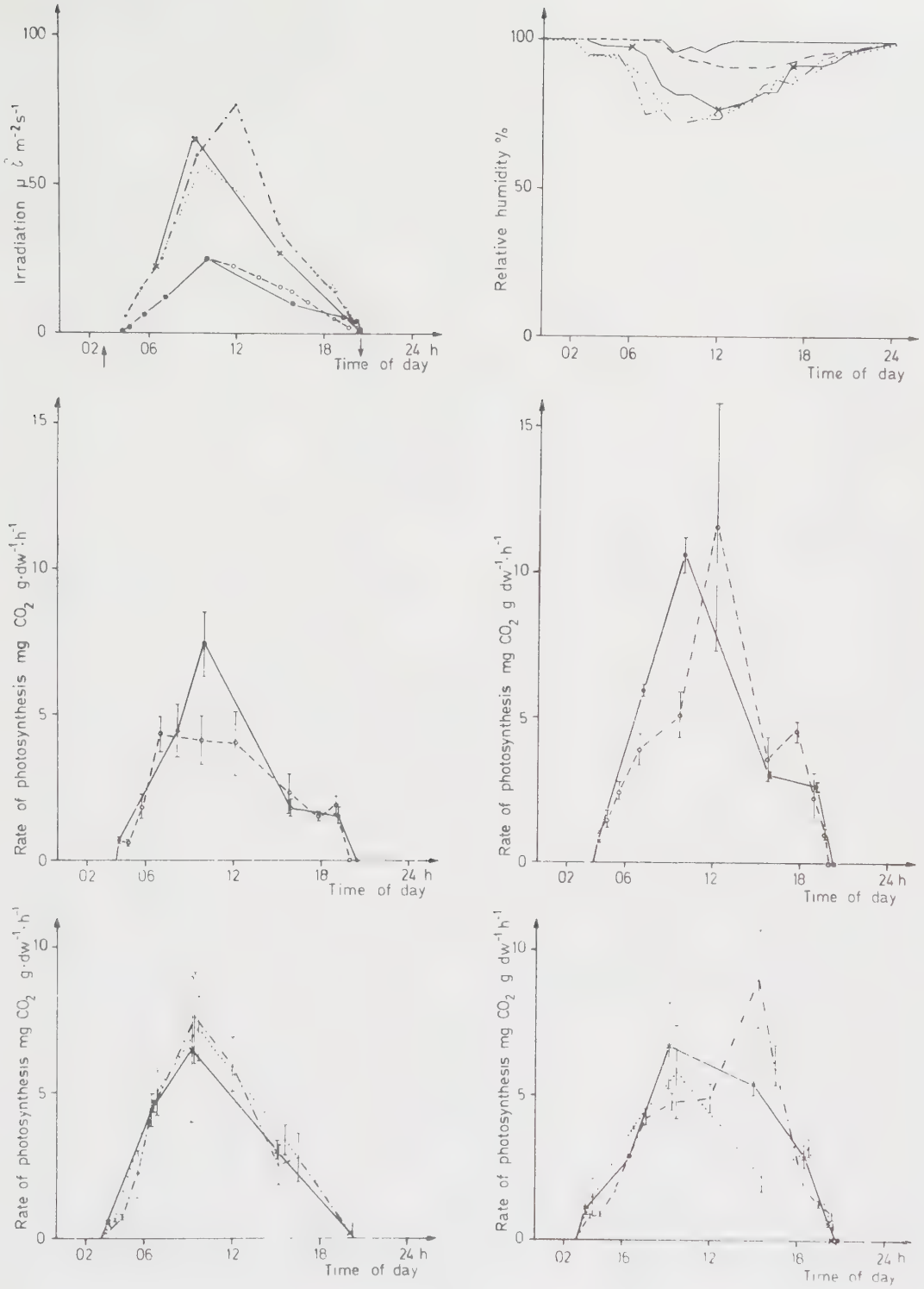


Figure 2a. Diurnal variation of irradiation, relative humidity and gross photosynthetic rate of Pleurozium schreberi (to the left) and Ptilium crista-castrensis (to the right) on May 1976. Sunrise(↑) and sunset(↓) are indicated in the figure. Symbols: Plot No.1 ————, plot No.2 - - - -, plot No.3 ....., plot No.4 -.-.-, and plot No.5 x———x.

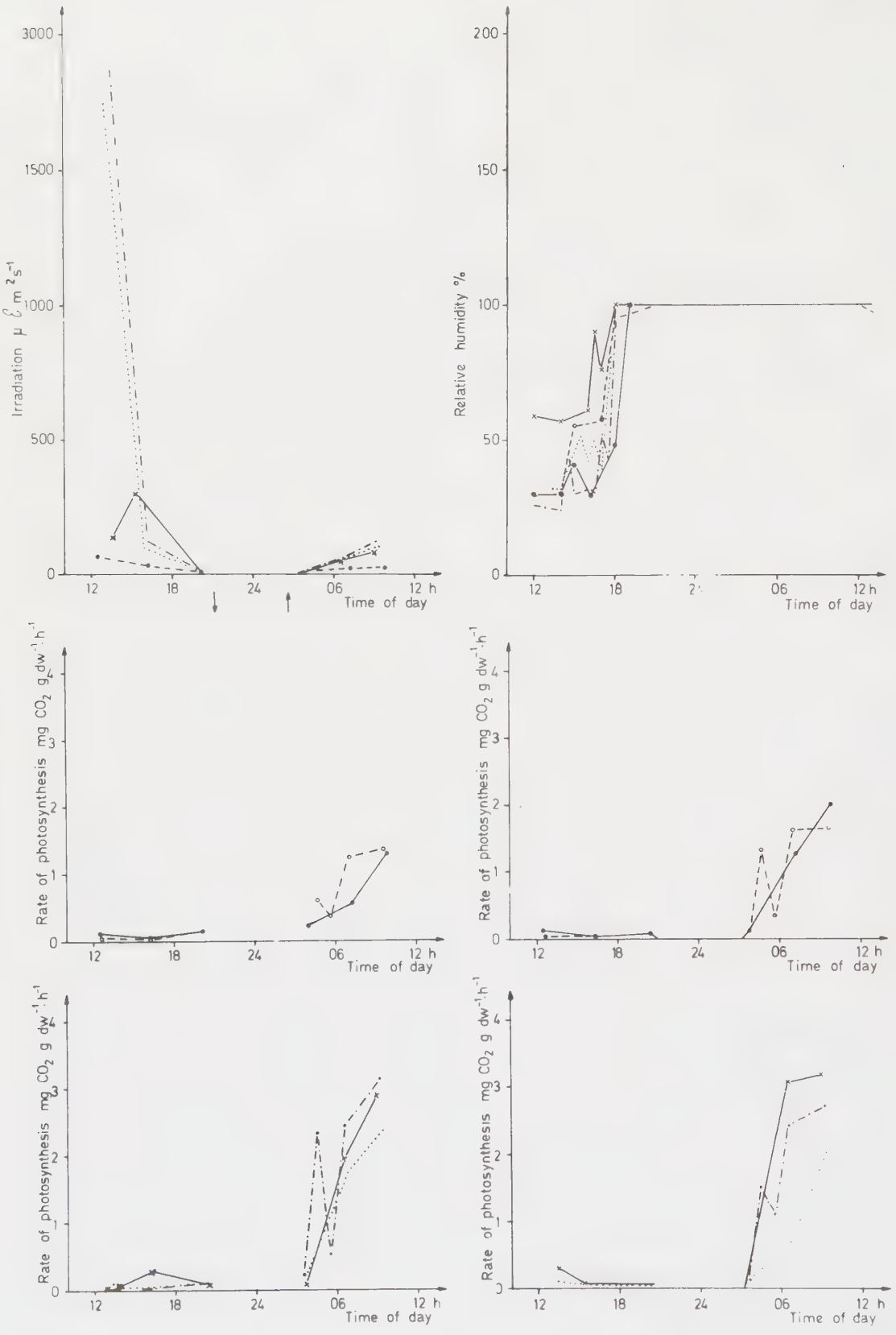


Figure 2b. Diurnal variation of irradiation, relative humidity and gross photosynthetic rate of Pleurozium schreberi (to the left) and Ptilium crista-castrensis (to the right) on 17-18 June 1976. Sunrise (↑) and sunset (↓) are indicated in the figure. Symbols: Plot No.1 ———, plot No.2 - - -, plot No.3 ....., plot No.4 -.-.-, and plot No.5 x———x.

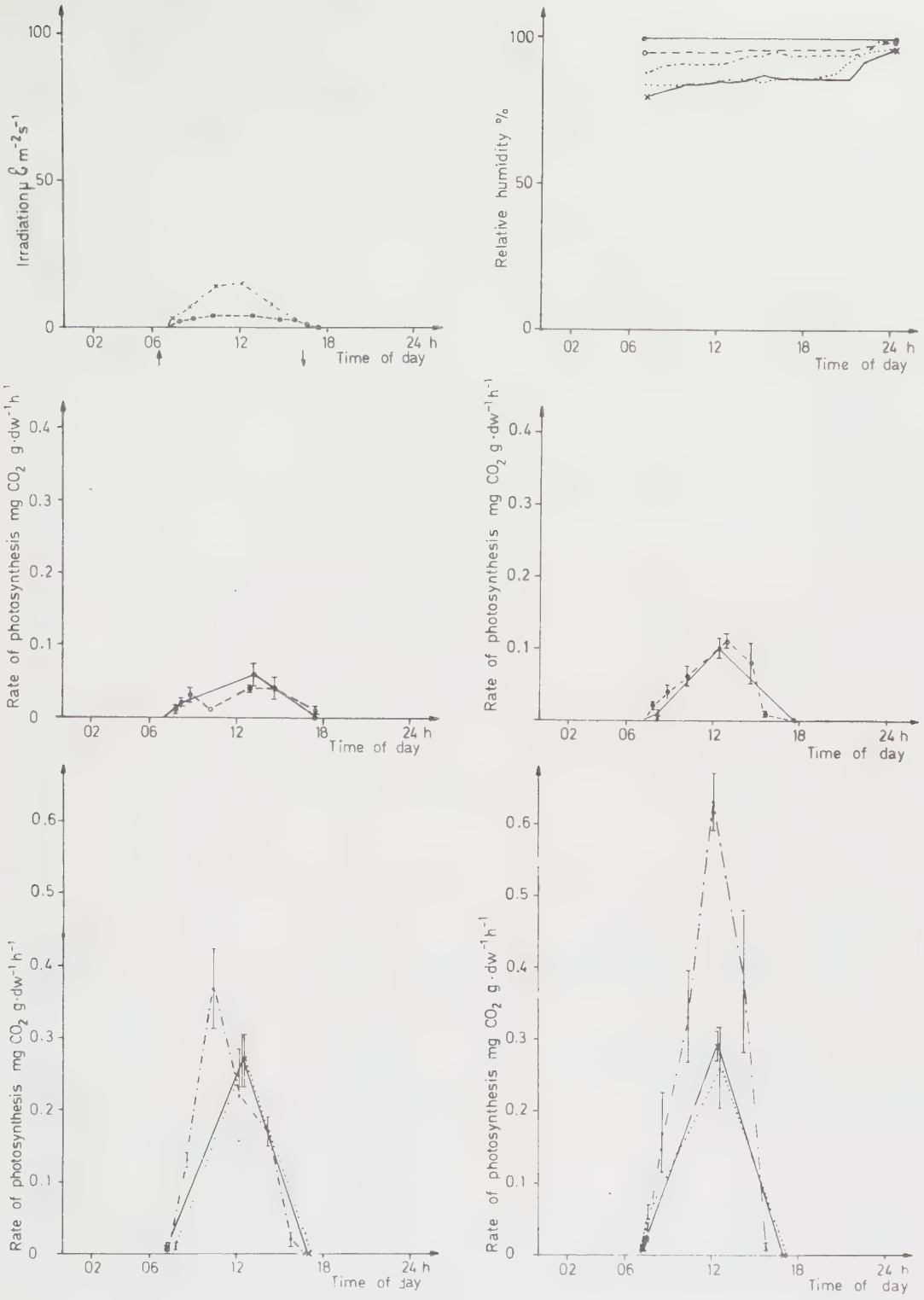


Figure 2c. Diurnal variation of irradiation, relative humidity, and gross photosynthetic rate of Pleurozium schreberi (to the left) and Ptilium crista-castrensis (to the right) on 22 October 1976. Sunrise(↑)and sunset(↓)are indicated in the figure. Symbols: Plot No.1 ———, plot No.2 - - -, plot No.3 ....., plot No.4 -.-.-.- and plot No.5 x———x.

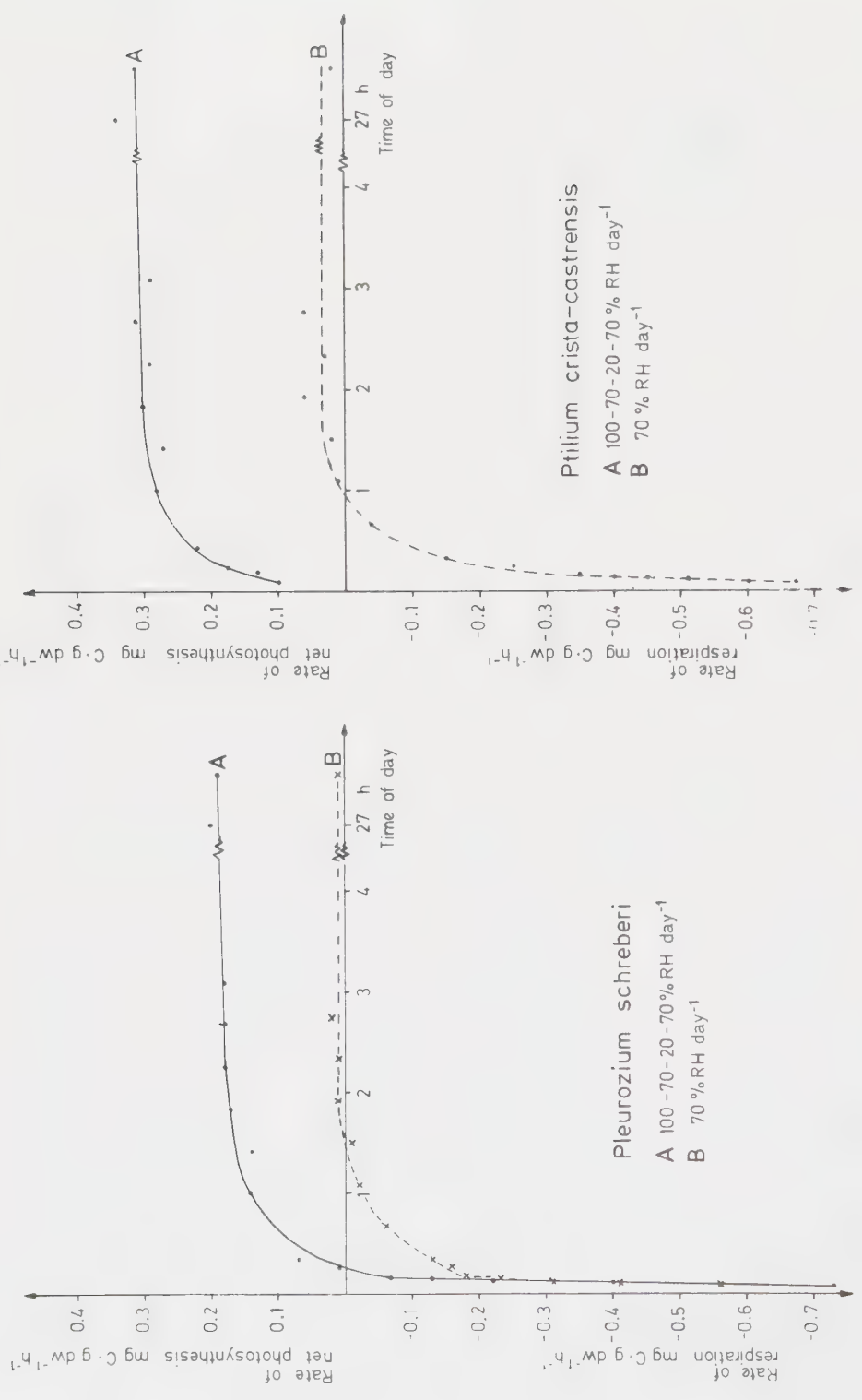


Figure 3. Rate of respiration and net photosynthesis of Pleurozium schreberi and Ptilium crista-castrensis after one week with decreased relative humidity.

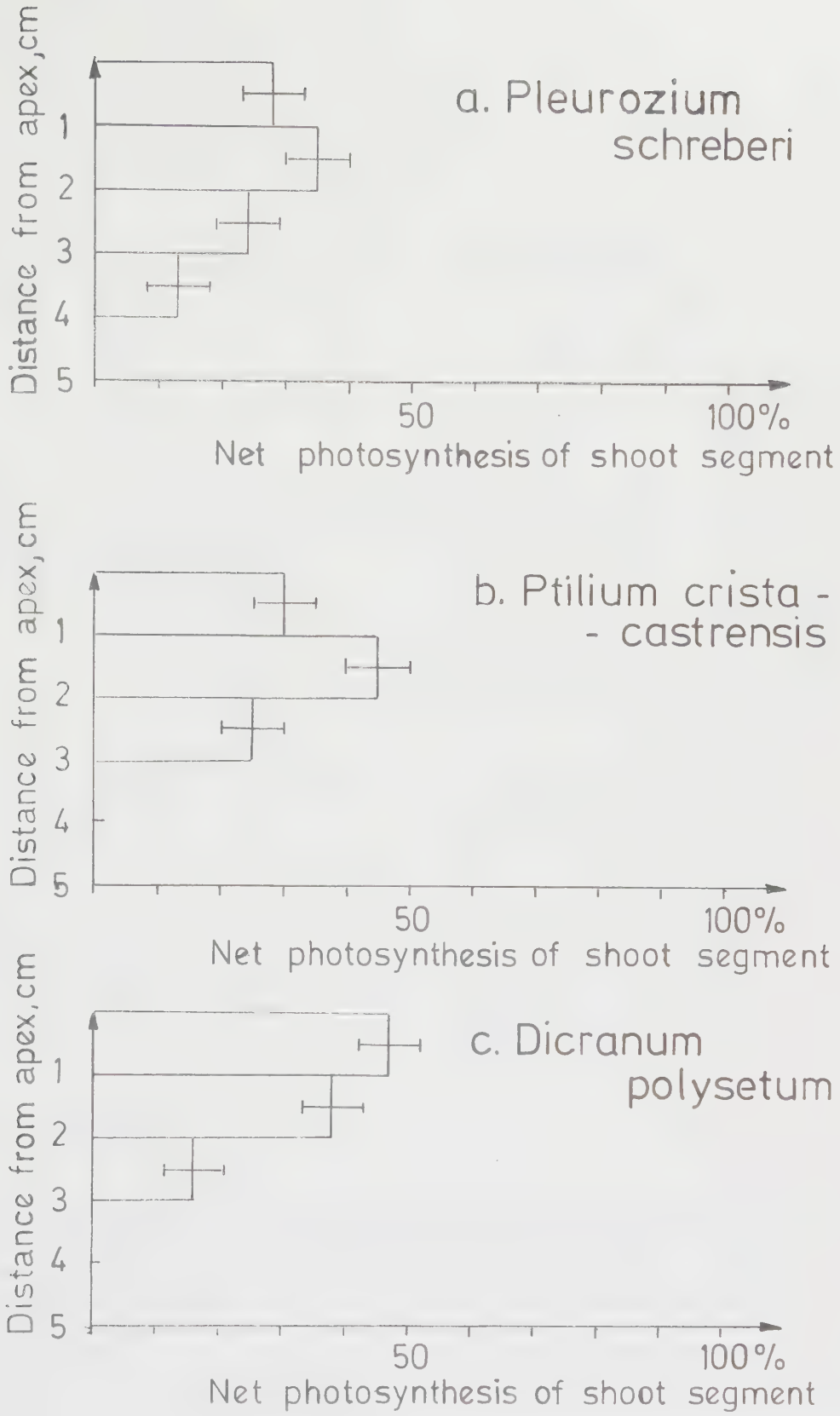


Figure 4. Net photosynthetic ability of shoot segments at different distances from the apex of three coniferous forest mosses, expressed as percent of the total shoot net photosynthesis.

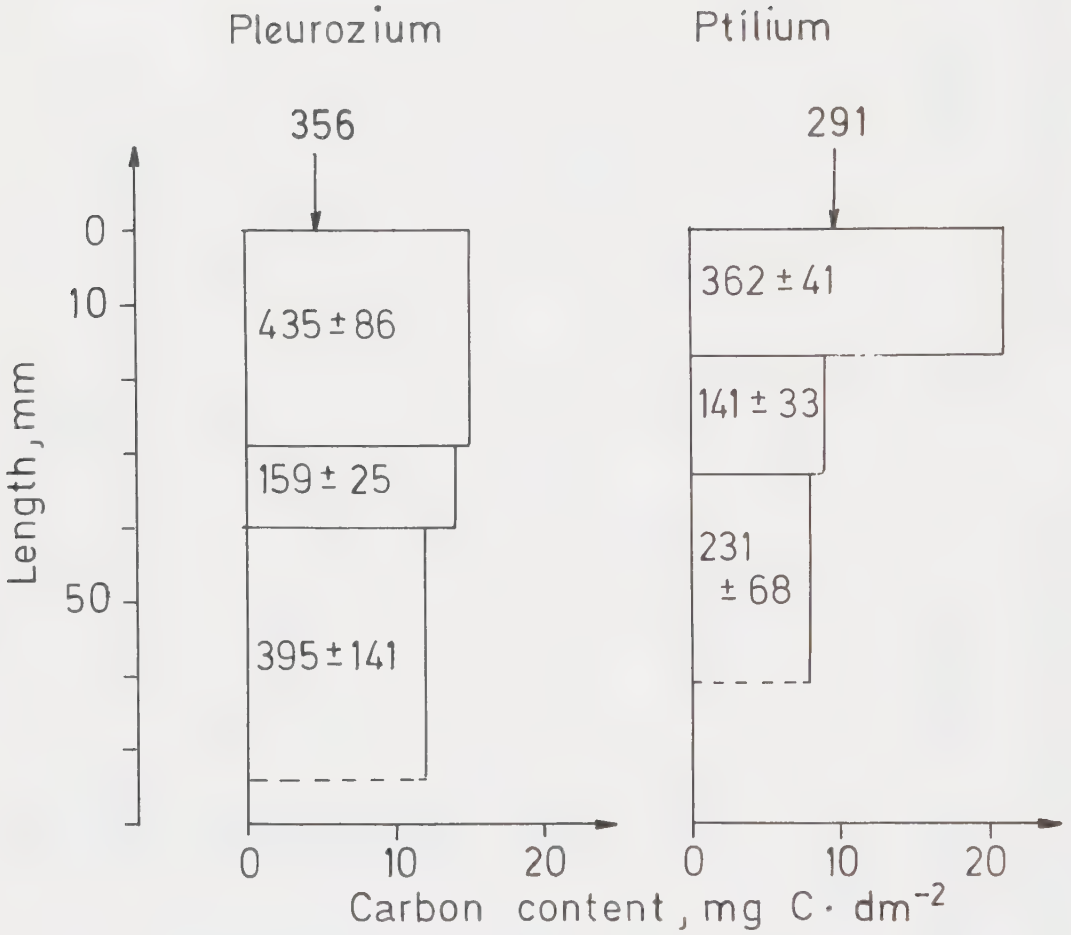


Figure 5. Average length and carbon content of different parts of Pleurozium schreberi and Ptilium crista-castrensis shoots estimated in June. The annual growth is taken from Table 1 a-b. The parts are from the top: "Illuminated" part,"green" part and "attached dead". Annual growth is characterised with an arrow.

EFFECTS OF SILVICULTURAL HERBICIDES ON THE PHOTOSYNTHESIS OF SEVEN BRYOPHYTE SPECIES

Ingrid Stjernquist

Dept. of Plant Ecology
Helgonavägen 5
S-223 62 LUND
Sweden

Torleif Ingelög

Dept. of Ecology and Environmental Research
Swedish University of Agricultural Science
S-750 07 UPPSALA
Sweden

ABSTRACT

Bryophytes form an important part of the non-target vegetation which might be influenced by chemical thicket control. Dicranum polysetum, Hylocomium splendens, Pleurozium schreberi, Pohlia nutans, Polytrichum commune, Rhytidiadelphus loreus and Sphagnum squarrosum were treated in the laboratory with 2, 4-D, MCPA, Triclopyr and Glyphosate in concentrations corresponding to the normal dose (N) used in practice. The herbicides gave selective effects on assimilation and respiration rate depending on moss species and compound. The phenoxy herbicides and Triclopyr caused an immediate and transitory reaction compared to Glyphosate. The colonist species, Pohlia, was affected only to a small extent and similarly for all herbicides. Polytrichum, with protective leaf structures,significantly decreased net photosynthesis after one month. Of the other moss species, Pleurozium was the most sensitive to 2,4-D, Hylocomium to MCPA and Sphagnum to Triclopyr. Glyphosate decreased CO_2 incorporation of Dicranum, Pleurozium, Polytrichum and Rhytidiadelphus to 30-50% of the control. Concentrations up to 0.5N Glyphosate and 1/8N 2,4-D stimulated photosynthesis of Dicranum and Pleurozium, respectively. Varying tolerance to herbicide and environmental factors as well as different abilities to recover might cause changes in the composition of the bottom layer. This conclusion was supported by a pilot field study with Dicranum and Pleurozium.

1 INTRODUCTION

Chemical thicket control is one of the techniques for direct vegetation regulation that have been used in management of northern coniferous forests for about three decades (Bärring 1978). Foliage spraying of herbicides on forest regeneration areas is performed in order to promote the growth of young conifers. The thicket, consisting of shrubs and young trees of various deciduous species, is the target of such operations. Other components of the vegetation might inadvertently be subjected to the herbicide treatment and thus influenced (Ingelög 1978).

Bryophytes often form a major part of the bottom layer vegetation of forest areas where herbicide spraying might occur. While herbicidal effects on higher plants have been rather intensively studied, effects on bryophytes seem to have been almost totally neglected.

The aims of this investigation were to determine whether four different herbicides, 2,4-D, MCPA, Tricolopyr and Glyphosate, affected the CO_2-exchange of seven common Swedish moss species, and whether climatic conditions modified such effects. Changes in population dynamics of the moss species after herbicide application will also be discussed.

2 MATERIALS AND METHODS

2.1 The herbicides

Of the four herbicides used in the investigation, two were phenoxy compounds. These were the esters of 2,4-dichlorophenoxyacetic acid (2,4-D) and 4-chloro-2-methylphenoxyacetic acid (MCPA). The other herbicide compounds were Roundup containing the active ingredient N-(phosphonomethyl) glycine (Glyphosate) and the amine of 3,5,6-trichloro-2-pyridyloxyacetic acid (Triclopyr). Only the first three compounds have hitherto been used in practice for chemical thicket control.

2.2 Sample collection

The seven bryophyte species used in this investigation are common in forests and in most of Sweden. Five of the species occur in coniferous and mixed forests. - Pleurozium schreberi (Brid.) Mitt., Hylocomium splendens (Hedw.)Br.Eur. and Dicranum polysetum Sw. are dominant on the forest floor: Sphagnum squarrosum Crome. and Polytrichum commune Hedw. grow in wet forests. Rhytidiadelphus loreus (Hedw.) Warnst. is common in deciduous and coniferous stands and Pohlia nutans (Hedw.) Lindb. is an early colonist found on dry open soil in various ecosystems.

Material for spraying experiments in the laboratory was collected from the following sites:

Species:	Forest type:	Locality:
Dicranum	Open Scots pine[1]	NW of Kalmar (56°45'N 16°10'E)
Hylocomium	" " "	- " -
Pleurozium	" " "	- " -
Sphagnum	Wet pine-spruce[2]-birch[3]	- " -
Polytrichum	" " "	- " -
Rhytidiadelphus	Pine-spruce-birch	S of Uppsala (59°39'N 17°44'E)
Pohlia	Spruce-birch	E of Lund (55°40'N 13°25'E)

[1] = Pinus sylvestris L. [2] = Picea abies (L.)Karst.

These reference areas were about 0.25 ha each and pure tufts of the seven moss species were randomly collected over the area.

Pleurozium and Dicranum were also collected from four reforestation areas of about 5 ha, at intervals of 3 months and 1 year following practical herbicide application. Two of the areas, Kärrstorp and Årtebäck, are situated NW of Kalmar. Before the spraying these areas had about 1-2 m high thickets dominated by birch. Spraying from a tractor was done in August 1979 with a buthoxyethyl ester formulation of 2,4-D. The other two areas are situated near Åtvidaberg ($17^{\circ}15'$N $59^{\circ}20'$E). They were sprayed with Glyphosate (Roundup) from a helicopter at about the same time. One of the sites, Kungsbäck, is a former pasture with groups of juniper (Juniperus communis L.) and scattered broad-leaved trees and with a 2-3 m high thicket dominated by aspen (Populus tremula L.). The other site, Bersbo, had a dense 3-4 m high mixed stand of Norway spruce, oak (Quercus robur L.) and aspen. Material was collected from randomly chosen points in each stand and from comparable reference stands in the neighbourhood.

2.3 Laboratory experiment

2.3.1 Herbicide treatment

From the reference samples small tufts of each moss species were randomly chosen and put together in a box of 2 dm^2. Tufts of Dicranum, Hylocomium, Pleurozium, Pohlia, Polytrichum, Rhytidiadelphus and Sphagnum were sprayed in the laboratory with normal doses (N) of Glyphosate, 2,4-D, and Triclopyr. Tufts of Hylocomium, Pohlia, Polytrichum and Rhytidiadelphus were also exposed to normal doses of MCPA. The herbicide concentrations were those recommended for application by plane or tractor, i.e.

Glyphosate	3 l in 300 l water	(360 g active ingredient l^{-1})
2,4-D	5 l in 500 l water	(500 g " " ")
MCPA	3 l in 500 l water	(500 g " " ")
Triclopyr	5 l in 500 l water	(360 g " " ")

The two dominating moss species in the bottom layer of the reference area near Kalmar, Pleurozium and Dicranum, were treated with varying concentrations of Glyphosate and 2,4-D. The 2,4-D concentrations range from 1/16 N to 5N for Pleurozium and from 1/2N to 5N for Dicranum. Both mosses were sprayed with 1/2N to 10N Glyphosate.

Before herbicide application the shoots were exposed to air humidity for one hour. From each treatment 2 x 40 shoots of the investigated moss species were randomly collected and cut to a length of 4 cm. The control samples were taken from the box just before herbicide application. Net photosynthesis and dark respiration were determined after 1 hour, 1 week and 1 month. Between the registration occasions the bryophytes grew in constant climate (430 $\mu E\ m^{-2}s^{-1}$, 10°C and 100% RH).

The effect of Glyphosate and 2,4-D treatment in the field on photosynthesis and respiration of Pleurozium and Dicranum was determined in the samples from the four reforestation areas near Kalmar and Åtvidaberg. Samples of 2 x 40 shoots of each species and area were randomly collected from the pure moss carpets and cut to a length of 4 cm. Comparison was made with materials from neighbouring reference areas.

2.3.2 The energy reserve

The ability of a typical coniferous forest bryophyte to maintain photosynthetic capacity by means of energy reserves was determined for Pleurozium. Nine parallel pots with 40 shoots each were placed in complete darkness, 20°C and 100% RH for varying times between 10 and 100 days. After dark periods, net photosynthesis and respiration were registered.

2.3.3 CO_2 exchange analysis

Just before the analysis, the mosses in the experimental pots were sprayed with water to optimum water content and then placed in plexiglass cuvettes with constant climate

(730 µE $m^{-2}s^{-1}$, 15°C and 100% RH). Net photosynthesis and respiration rate were determined using gas exchange technique, CO_2 being detected with an infra-red analyser (URAS 2), coupled to a continuous air flow system through the cuvettes. At the end of the experiment, the dry weight of the mosses was estimated (85°C, 24 hours).

2.4 The variation of the material

The standard deviation of measurable values obtained with the laboratory method was investigated in a separate study with moss shoots from the reference areas. The standard deviation was found to vary 9-11% of the mean value in determinations of net photosynthesis, depending on species, and to be 12% in determinations of respiration (n=9).

2.5 Field experiment

In June 1979, two months before practical herbicide application with 2,4-D, four experimental plots of 0.5 x 0.5 m were randomly placed in each of the reforestation areas in Kärrstorp and Årtebäck. Cover percentages of Pleurozium and Dicranum were determined. Changes in vigour of the three moss species expressed as differences in morphology and colour compared to June, were examined in November 1979 and September 1980 and the cover percentages of Pleurozium and Dicranum were calculated in September 1980.

Biomass per unit area in pure carpets of Pleurozium and Dicranum on the reference site near Kalmar was determined with frames of 1 dm^2. Ten samples of each species were punched and the dry weight of the green part of the shoots registered (85°C, 24 hours).

2.6 Calculations

Student´s t-test was used to test the differences in photosynthesis between Pleurozium and Dicranum samples treated with varying concentrations of 2,4-D and Glyphosate. Changes in diurnal CO_2-exchange of the seven moss species after herbicide spraying with normal dose were calculated from the long-term values in the laboratory experiment. The climatic conditions of an autumn day, typical for the situation after the practical herbicide spraying in late August, were simulated. The long-term herbicide effect in situ developed during a period with climate conditions near optimum for bryophyte growth. The hypothetical day had 12 hours' light and 12 hours' darkness and the water content in the moss shoots was assumed not to restrict photosynthesis. The diurnal CO_2 exchange of untreated Dicranum was given the value 1, because this bryophyte can be found in the most combinations with some of the other bryophytes. The other moss species are related to Dicranum.

If the reforestation area was treated with herbicides earlier in the summer, e.g. in mid-June, the characteristics of the hypothetical day changed. On clear summer days, most bryophyte species only photosynthetize about five hours in the morning on account of desiccation (cf. Stjernquist 1981a). The summer nights in the southern part of Sweden range from 5.5 hours in June to 10 hours in late August.

Rewetting after a period of drought in summer gives a respiration of about twice the maximum rate of normal conditions (cf. Hinshiri and Proctor 1971, Peterson & Mayo 1975). This burst of respiration is reported to be of short duration and, in this study, was assumed to last for one hour.

3 RESULTS

3.1 Effects of normal dose

The photosynthetic reactions of the studied moss species to normal doses of 2,4-D, MCPA, Triclopyr and Glyphosate are shown in Table 1. The photosynthetic process affected, and the degree of influence depended on species and the herbicide used. Only a few general characteristics can be identified in the results, the most important being that the phenoxy herbicides and Triclopyr gave a more immediate and transitory effect compared to Glyphosate.

2,4-D and MCPA

Pleurozium was the species most affected by 2, 4-D. After one hour, the assimilation rate decreased by 70% of the control value and respiration increased by the same value. One month later, the processes had started to recover. Sphagnum reacted in a similar way, but the immediate decrease in assimilation was rather small. The CO_2 incorporation of Hylocomium and Pohlia continued to decrease throughout the experiment. The maximum value was about 30%. The respiration rate of Dicranum was stimulated by the herbicide, while the assimilation was not significantly influenced. A clearly negative long-term effect of 2,4-D on CO_2 fixation was registered for Polytrichum and Rhytidiadelphus.

MCPA caused severe injury to Hylocomium. One hour after application, respiration was about twice as high as the control, but assimilation was only 40% and remained low during the experimental period. The reaction of Pohlia, however, resembled that of 2,4-D treated shoots. Polytrichum and Rhytidiadelphus increased respiration by 30%, but only Polytrichum maintained a high value after one month.

Triclopyr

The main effect of the herbicide on the seven moss species, except for Pohlia, was a stimulation of the respiration rate.

The assimilation rates of Hylocomium, Pleurozium and Sphagnum immediately decreased by about 30-40%, but in the first two species the influence was of short duration and the mosses had started to recover after one month. The CO_2 incorporation of Dicranum, Polytrichum and Rhytidiadelphus was not significantly changed by Triclopyr application. The effect of the compound on Pohlia was similar to that of the phenoxy compounds.

Glyphosate

In Pohlia only the respiration rate changed significantly when the moss was treated with Glyphosate. After one month the CO_2 incorporation of Dicranum, Pleurozium, Polytrichum and Rhytidiadelphus decreased to low values, 30-50% of the control. The CO_2 fixation in Sphagnum, however, was significantly stimulated by the normal dose of Glyphosate. The low respiration value of Pleurozium is probably incorrect, because a herbicide concentration of ½N only gave a decrease of 15%.

3.2 The effects of varying concentrations of herbicides

One hour after 2,4-D application the net photosynthesis of Pleurozium was negatively related to the herbicide concentration from 1/16N to 5N (Figure 1a). The decrease was significant ($p < 0.05$) at 1/4N. Dicranum, however, was unaffected at concentrations lower than the normal dose. After one week the photosynthetic process of both moss species seemed to recover from all the treatments, with the exception of Pleurozium sprayed with 5N 2,4-D (Figure 1b). As a long-term effect, low concentrations of the herbicide, 1/16 to 1/8N, stimulated photosynthesis of Pleurozium but high concentrations, 5N, still inhibited CO_2-exchange.

Glyphosate had an immediate minor effect on Pleurozium compared to 2,4-D but a concentration of 5N significantly decreased photosynthesis ($p < 0.05$). The CO_2 uptake of Dicranum, however, was stimulated at all concentrations but only normal dose gave a significant increase ($p < 0.05$). After one month, this concentration

decreased the net photosynthesis of Dicranum to a value of one-fifth of the control whereas a lower dose stimulated the process. The CO_2-fixation of Pleurozium was negatively related to herbicide concentrations up to normal dose.

3.3 Field studies

Three months after herbicide application with a normal dose of 2,4-D in situ, the net photosynthesis of Pleurozium showed a lower value compared to the long-term results with the analogous concentration in the laboratory experiment (Table 2). Dicranum, however, had a higher CO_2 uptake than the control sample. After one year, the photosynthetic rate of living Pleurozium shoots had risen to twice the value, and Dicranum on one site, Årtebäck, had continued to increase.

On the Glyphosate-treated sites, Kungsbäck and Bersbo, the CO_2 fixation of Pleurozium in November 1979 was inhibited and at Kungsbäck this inhibition was of the same magnitude as in the laboratory. Dicranum was not significantly affected. In September 1980, both moss species at Kungsbäck had a higher photosynthesis rate.

The differences in responses of Pleurozium and Dicranum to 2,4-D had changed the cover percentage of the mosses in September 1980 (Table 3). The living fraction of Pleurozium had decreased by 5%, on average, while the Dicranum population had a corresponding increase.

The months after 2,4-D application, Pleurozium in the ten experimental plots had a brownish discolouration, and Dicranum had scattered brown patches on the leaves. In the depressions of Kärrstorp, foliar chlorosis occurred in Sphagnum while Polytrichum did not show any visible changes.

About a year later, only the current-year shoots of Pleurozium were green and had grown out only from the top bud (Figure 2).

About half the number of Dicranum individuals had developed lateral shoots, while the others continued to grow from the apex. Current-year shoots were dark green and seemed to be vigorous, while the older parts still were affected (Table 2). Sphagnum was in poor condition and had generated only a few thin current-year shoots from the lower part of the moss carpet. The upper part was dead (Figure 3).

No visible changes in the vigour of the Pleurozium and Dicranum shoots could be seen until one year after the Glyphosate treatment. At that time the Pleurozium shoots at Kungsbäck had turned brown and, in contrast to those sprayed with 2,4-D, there was no distinction between current-year segments and the older parts.

3.4 The energy reserve of Pleurozium

A period of up to ten days in complete darkness did not significantly affect the net photosynthetic ability of Pleurozium (Figure 4). Between the 10th and the 20th day, assimilation and respiration decreased by 40%. CO_2 incorporation continued to decrease until 100 days after the start of the experiment and then stopped. Respiration was nearly constant between 10-65 days but then increased again. The CO_2 exchange was positive for 90 days.

3.5 The diurnal photosynthetic production

In a bottom layer with mosses unaffected by herbicides, the diurnal production at optimum water conditions of the seven moss species increased in the order Dicranum - Pleurozium - Rhytidiadelphus - Sphagnum - Hylocomium - Polytrichum - Pohlia (Table 4). When treated with a normal dose of Glyphosate, the relationship between the species remained unchanged with the exception of Sphagnum. This bryophyte increased its production twice and thereby reached that of Pohlia. In the other species the diurnal value decreased and Dicranum and Pleurozium were relatively more depressed than the other bryophytes.

The phenoxy compounds changed the relative positions of Pohlia and Polytrichum compared to untreated samples. The CO_2 fixation of Rhytidiadelphus and Hylocomium were the most negatively affected by 2,4-D and MCPA, respectively.

Triclopyr caused a low diurnal production of Sphagnum, which only attained 30% of the control. Pleurozium, Dicranum and Rhytidiadelphus remained almost unaffected by herbicide treatment.

The relative order of the diurnal production of all the investigated moss species respectively, when treated with 2,4-D at varying times of the year, as well as after a desiccation period, remained unchanged throughout (Table 5).

4 DISCUSSION

4.1 The photosynthetic reaction after herbicide application

Several authors have discussed the selective effects of the herbicides Glyphosate, 2,4-D, MCPA and Triclopyr on higher plants (cf. Åberg & Eliasson 1978, King & Radosevich 1979, Lund-Høje 1979, Oorschot, van 1979). Possible explanations of the herbicidal effects seem to be related to four major steps of herbicide action in the plant species, i.e. (a) absorption and penetration of the leaf surface; (b) transport inside the plant; (c) breakdown of the cell walls and cell membranes; (d) toxic effects inside cells (Allebone et al. 1975).

For higher plants the first two steps determined the amount of herbicide which reaches the cells. The protectional structures of the leaves, like wax-layers and cuticle, which decrease water loss through diffusion and transpiration, also act as an external protection against herbicide application more or less effectively depending on species (cf. Hammerton 1967, Withwell et al. 1980). When the compounds do not directly affect the photoreactions, the extent of damage after herbicide treatment also depends on

the amount transported to actively growing points, etc. This is assumed to be valid for the four herbicides investigated.

Of the seven moss species Polytrichum seems to be the only bryophyte which has leaves with thicker cuticle and wax-layer (Bayfield 1973) and has developed conductive tissue inside the shoot for translocation of organics and water (cf. Callaghan et al. 1978, Sheirer 1980). Polytrichum receives water both directly from precipitation as well as through its internal system. The increased herbicide effect with time shown by Polytrichum for the four investigated compounds indicates that for this species the leaf surface will partly prevent herbicide penetration. Transport of herbicide inside the shoots and to the underground system may also be possible.

The other six species take up water only through the leaves and depend on rainfall, dew and high humidity to reach water contents sufficient for photosynthesis (cf. Stjernquist 1981a). The moss leaves are therefore very thin, allowing a rapid absorption rate. Because the herbicides are applied in water, the leaf surface probably does not constitute a barrier to herbicide penetration. In these kinds of mosses the herbicide effect may be restricted mainly to the application spots. Because spraying takes place in dry weather the external capillary water conduction between the leaves and stem which exists during rainfall will be of no significance for enhancing the herbicide effect. The morphology of the mosses cause the herbicide to fall on different parts of the shoot. Thus, for Hylocomium and Pleurozium only the mature parts are affected while the smooth and solid top bud is probably water repellent and remains green and rather vigorous. In contrast, the young and upper part of, for instance, Sphagnum and Dicranum, receives most of the herbicide droplets and thus decreases in vigour.

The discussion indicates that, with the exception of Polytrichum, the selective reaction of moss species to herbicides may be the effects of possible changes in cell walls and membranes, in concentration levels inside the cells and in the resistance to the specific herbicide.

The selective response in net photosynthesis of the investigated bryophytes after herbicide application seems to be primarily due to differences in assimilation rate. Although the relative increase in respiration for the seven moss species in many cases is rather high, especially when treated with phenoxy herbicides and Triclopyr, the real carbon loss is small compared to uptake by assimilation. In some cases, however, only the respiration process significantly changes, as in the cases of Dicranum treated with 2,4-D, MCPA and Triclopyr, and Polytrichum and Rhytidiadelphus treated with the last two compounds.

The CO_2 incorporation of the colonist species, Pohlia, is only affected to a small extent and similarly for all herbicides. This may partially depend on the thick cell walls (Nyholm 1958) but more probably the moss species is able to physiologically withstand herbicide concentrations that are toxic to other species.

Generally, the coniferous forest species - Dicranum, Hylocomium, Pleurozium and Sphagnum - seem to be negatively influenced for a relatively short time when treated with 2, 4-D, while Glyphosate gives a long-term effect.

Martin & Fletcher (1972) and Kleudgen (1978) have found that 2,4-D and MCPA reduce chlorophyll concentration in higher plants. The decreased assimilation rate in the experiment for Pleurozium, Hylocomium and Sphagnum treated with 2,4-D and MCPA, together with chlorosis in the moss shoots, indicates that the phenoxy herbicides also affect the chlorophyll content in the moss shoot and that this may be an important factor for inhibited net photosynthesis. The negative reaction of the moss species to Triclopyr could probably involve the same mechanism, because the chemical composition of Triclopyr is very similar to these herbicides. Dicranum, however, differs from the other coniferous bryophytes because the phenoxy herbicides mainly affect the respiration process.

The long-term effect of Glyphosate on assimilation seems to depend on changes in several physiological processes that

indirectly inhibit the photosynthetic ability (cf. Jaworski 1972, Kells et al. 1979, Richard et al. 1979). The net photosynthesis of Hylocomium, Pleurozium and Dicranum was depressed in this investigation, in the latter two species to the same degree, but the registered value may conceal a selective response that, for instance, would be of importance for the recovery of the bryophyte.

The morphology of Polytrichum, as compared to the other coniferous forest mosses, gives a reaction to herbicide application that more resembles that of higher plants. A minor immediate effect on net photosynthesis of both herbicides, Triclopyr and Glyphosate, indicates that the wax layer and cuticle of the leaves (Bayfield 1973) will be a barrier to herbicide penetration (Lund-Høje 1979). The experimental method with cut moss shoots may, however, give an underestimation of the long-term effect on the bryophyte, because transport to and the reaction of the underground system following herbicide application cannot be studied.

4.2 Growth regulation

The competitive ability of a specific moss species is considered to be related to net productivity (cf. Black et al. 1969, Stjernquist 1981b). In an ecosystem where some of the investigated bryophytes co-exist in the bottom layer, the dynamics between the species in a certain habitat may be dependent on the diurnal CO_2 fixation of each species and possible changes caused by environmental variables. The long-term effect on growth after herbicide application may be assumed to be an effect of the quantity of herbicide that reaches the moss carpet, the duration of the specific herbicide reaction and the joint effect of herbicide and climatic variables. With the exception of Pohlia and Polytrichum, the long-term effect of the phenoxy compounds and Triclopyr in the studied moss species, at optimum water conditions, is not especially evident, probably because the herbicide concentration in the moss shoot has decreased. Eronen et al. (1979) found that the MCPA content in Pleurozium samples decreased to 7% of the starting concentration six weeks after spraying.

Pleurozium and Dicranum are the dominating species in the bottom layer of the investigated areas. The photosynthetic reaction of these species mainly determines the CO_2 incorporation of the moss carpet following herbicide application. Spraying a reforestation area with a normal dose gives a wide variation in the herbicide coverage of the bottom layer, depending on the structure of the thicket (Ingelög 1978) and the often uneven application. In the long run this gives a mosaic influence on the net production in the moss layer and increases the variation over the area.

During herbicide treatment in situ at normal doses, the most common concentrations reaching the moss carpet probably vary between 1/4N and 2N. Within this range, the photosynthetic capacities of Pleurozium and Dicranum change independently of each other, expecially when Glyphosate is used. Even if the total CO_2-fixation into the moss layer increases, the relative competitive ability of the species probably alters in comparison with the reference area. Thus, when using Glyphosate concentrations lower than the normal dose, Dicranum seems to be promoted compared to Pleurozium. With 2,4-D, however, there is a tendency for stimulation of Dicranum only at 0.5N. The difference in photosynthesis of a single moss species demonstrated by the samples from the four reforestation areas, indicates that the bottom layer has been subjected to a varying dose of herbicide.

The photosynthetic process of the seven moss species investigated has varying sensitivity to the climatic variables, especially desiccation (cf. Tamm 1953, Peterson & Mayo 1975, Callaghan et al. 1978). The photosynthetic capacity of the untreated mosses at optimum climatic conditions is assumed to show the diurnal CO_2 exchange at maximum competitive ability (Table 3a). The ability of a certain bryophyte to compete after application of a specific herbicide may then be dependent on the relation between the diurnal net production of the control and the affected mosses, i.e.:

$$C = \frac{P_A}{P_B}$$

where C = competitive ability, P_A = net production of the

affected moss and P_B = net production of the control.

The ratio seems to be the same during the vegetation period (Table 4). The competitive ability of a single species when influenced by micro-climate may be expressed as

$$C = f\frac{P_A}{P_C}$$

where the factor f is the decrease of diurnal CO_2 fixation caused by the climatic variables.

The herbicidal effect can be enhanced by the climate in two ways:

a. The herbicide may change the bryophyte, anatomically and morphologically, in a way that affects its response to climate.
b. A climatic factor and a herbicide may have additive physiological effects.

The first of those two ways is especially important for the ability of the bryophyte to absorb and maintain enough water for photosynthesis. Åberg and Eliasson (1978) and O'Brien and Prendeville (1979), for example, have reported that 2,4-D may directly change membrane permeability. Hylocomium, Pleurozium and Rhytidiadelphus, the species growing in more or less loose mats, probably have a faster water loss than species growing in tufts where moist conditions around the moss shoot decrease the desiccation rate. An increased permeability for water therefore may have a more negative effect on the photosynthesis of these species.

The second statement seems to be valid for bryophytes treated with Glyphosate. Glyphosate has been found to inhibit normal protein synthesis (Cole et al. 1979, Tymonko 1979, Hoagland 1980). Moss species sensitive to desiccation, like Hygrohypnum luridum, do not retain their ability for protein synthesis when rehydrated after drought (Gwóźdź & Bewley 1975). In summer, with rapid desiccation and long dry periods, the negative long-term effect of Glyphosate on moss production may be enhanced for sensitive terrestrial mosses. Pleurozium, for example, probably is severely affected by desiccation (cf. Stjernquist 1981a).

The joint effect of herbicide and climatic factors is also important because the micro-climate of reforestation areas often changes after herbicide application, when the thicket layer has disappeared. Irradiation to the ground increases and influences the relative humidity and temperature. The effect is demonstrated in the field studies at Kärrstorp and Årtebäck. After one year, the living fraction of the desiccation-sensitive species, Pleurozium, decreased more than the effect of a single 2,4-D application can explain, and the population structure of the moss carpet had changed compared to the situation before the spraying.

4.3 The recovery process

Besides the characteristics discussed above, the ability of survival and regrowth in a moss species after herbicide application may also be related to the energy reserve in the shoots. The great immediate inhibition of net photosynthesis in some of the coniferous forest mosses treated with phenoxy compounds involved a high CO_2 loss through respiration, which might also be increased by climatic variables. The mosses, however, seem able to withstand rather long periods with only respiration before their vigour drastically decreases. In the investigation this is exemplified by Pleurozium, which has to be placed in complete darkness for 18 days before the photosynthetic ability decreases to 50% of the control (Figure 2). The result indicates that when the phenoxy herbicide concentration in the moss shoots approaches zero, about six weeks after application (Eronen et al. 1979), there will probably be enough living parts to allow regrowth. The recovery process of the shoots had already started one month after application for most of the moss species, when growing at optimum climatic conditions. One year after 2,4-D spraying, the CO_2 exchange of Pleurozium in situ reached a value in the same order of magnitude as the control sample. Dicranum shows the same tendency in one of the experimental sites. When the negative herbicidal effect exists for a long time - as in Dicranum, Hylocomium, Pleurozium, Polytrichum and Rhytidiadelphus treated with Glyphosate, but also in certain moss species treated with phenoxy compounds - the shoots may be unable to recover.

Regrowth in the bryophytes, with no conductive tissue, starts either from the top bud - Pleurozium and Hylocomium - or from the lower parts of the shoot, as lateral shoots, as for example in Sphagnum. Dicranum can regrow in both ways, but in Polytrichum the conditions seem to be more complex, because new vegetative shoots are normally supported from older parts of the moss through an underground system (Callaghan et al. 1978). In higher plants, Glyphosate seems to be transported to the roots when applied to the leaves (cf. Fernandez & Bayer 1977, Whitwell et al. 1980). If the same process is valid for Polytrichum, the long-term effect of Glyphosate will restrict vegetative reproduction. However, when the moss is treated with phenoxy herbicides, the situation for regrowth is probably different. Köhler and Müller (1970), when working with Equisetum palustre, found that the transport of 2,4-D and MCPA to the rhizoids was very small after shoot application. The development of new shoots from the underground system of Polytrichum may then be unaffected.

5 CONCLUSIONS

- The four herbicides, 2,4-D, MCPA, Triclopyr and Glyphosate cause selective effects on the assimilation and respiration rate of the seven moss species investigated. This implies that when the moss carpet is sprayed with a certain herbicide the decrease of total CO_2-incorporation probably may be dependent on the species composition.

- A characteristic difference between the four herbicides seems to be that Glyphosate has a long-term influence on the CO_2-exchange while mosses treated with 2,4-D, MCPA and Triclopyr started to recover after one month. Glyphosate also decreases net photosynthesis to low values in most of the species examined. The only compound that mainly affected respiration is Triclopyr.

- The colonist species, Pohlia, slightly decreased net photosynthesis and similarly for all herbicides. The protective leaf structures of Polytrichum cause a small or insignificant

immediate effect on assimilation and respiration. The long-term reaction will be more severe. Of the other moss species the coniferous forest mosses, Pleurozium and Hylocomium, are most negatively influenced by herbicide treatment. Only in one case, i.e. Sphagnum sprayed with Glyphosate, was CO_2 incorporation stimulated.

- All herbicides probably change the relative competitive ability of the seven bryophytes. The amount of herbicide reaching the bottom layer, and the joint effect of climate seems to be of importance.

- The great energy reserve found for moss shoots is essential for recovery and regrowth. When the herbicide remained a short time in the moss layer, the net photosynthesis reached the control value after one year. A long-term herbicide effect, however, may result in the bryophyte being unable to recover. The morphology of the species influenced the regrowth of new shoots.

6 REFERENCES

Allebone, J.E., Hamilton,R.J. and Ravenscroft, B. 1975. Environmental Chemistry. In Eglinton, G. (ed.) The Chemical Society, London, vol. 1.

Bayfield, N.G. 1973. Notes on water relations of Polytrichum commune Hedw. J. Bryol. 7:607-617.

Black, C.C., Chen, T.M. and Brown, R.H. 1969. Biochemical basis for plant competition. Weed Sci. 17:334-338.

Bärring, U.S.M. 1978. The use of phenoxy herbicides in Swedish forestry: Amounts, types and modes of application. In Ramel, C. (ed.) Chlorinated Phenoxy Acids and Their Dioxins. Ecol. Bull. (Stockholm) 27:219-230.

Callaghan, T.V., Collins, N.J. and Callaghan, C.H. 1978. Photosynthesis growth and reproduction of Hylocomium splendens and Polytrichum commune in Swedish Lapland. Oikos 31:73-88.

Cole, D.J., Dodge, A.D. and Casely, J.C. 1979. Effects of glyphosate on protein synthesis and phenylalanine metabolism in rhizome buds of Agropyron repens. Plant. Physiol.(Bethesda) 63 (5 suppl.):96.

Eronen, L., Julkunen, R. and Saarelainen, A. 1979. MCPA residues in developing forest ecosystem after aerial spraying. Bull. Environ. Contam. Toxicol. 21 (6):791-798.

Fernandez, C.H. and Bayer, D.E. 1977. Penetration, Translocation and Toxicity of Glyphosate in Bermuda grass(Cynodon dactylon) Weed Sci. 25(5):396-400.

Gwóźdź, E.A. and Bewley, J.D. 1975. Plant desiccation and protein synthesis. Plant. Physiol. (Bethesda) 55:340-345.

Hammerton, J.L. 1967. Environmental factors and susceptibility to herbicides. Weeds. 15:330-336.

Hinshiri, H.M. and Proctor, M.C.F. 1971. The effect of desiccation in subsequent assimilation and respiration of the bryophytes Anomodon viticulosus and Porella platyphylla. New. Phytol. 70:527-538.

Hoagland, R. 1980. Effects of Glyphosate on metabolism of phenolic compounds: VI. Effects of Glyphosine and Glyphosate Metabolites on Phenylalanine, Ammonia-Lyase Activity, Growth and Protein, Chlorophyll and Anthocyanin levels in Soybean (Glycine max) Seedlings. Weed. Sci. 28(4): 393-400.

Ingelög, T. 1978. Effects of the silvicultural use of phenoxy acid herbicides on forest vegetation in Sweden. In Ramel, C. (ed.) Chlorinated Phenoxy Acids and Their Dioxins. Ecol. Bull. (Stockholm) 27:240-254.

Jaworski, E.G. 1972. Mode of action of N-(phosphonomethyl) glycine: Inhibition of aromatic amino acid biosynthesis. J. Agric. Food Chem. 20:1195-1198.

Jenner, C.F. 1963. The physiology of the action of 2,4-D. Rept. Waite. Agric. Res. Inst. 36:36-37.

Kells, J.J. and Rieck, C.E. 1979. Effects of illuminance and time on accumulation of Glyphosate in Johnson grass (Sorghum halepense). Weed. Sci. 27(2):235-237.

King, M.G. and Radosevich, S.R. 1979. Tanoak leaf surface characteristics and absorption of Triclopyr. Weed. Sci. 27(6): 599-604.

Kleudgen, H.K. 1979. Veränderung der Pigment- und Prenylchinongehalte in Chloroplasten von Gerstenkeimlingen nach Applikation des Wuchsstoffherbizids MCPA (4-Chloro-2-methylphenoxyessigsaure). Z. Naturforsch. B. 34:106-109.

Köhler, J. and Müller, F. 1970. Untersuchungen zur Translokation von ^{14}C-markierten Herbiziden in Equisetum palustre L. Zeitschrift Pflanzenkr. Pflanzenscutz. 77:429-437.

Lund-Høje, K. 1979. The physiological fate of Glyphosate-^{14}C in Betula verrucosa and Fraxinus excelsior. The effect of ammonium sulphate and the environment on the herbicide. Meld. Nor. Lantbrukshögsk. 58(30) 24 pp.

Martin, J.A. and Fletcher, J.T. 1972. The effect of sublethal doses of various herbicides in lettuce. Weed. Res. 12(3): 268-271.

Nyholm, E. 1958. Musci In: The Illustrated Mossflora of Fennoscandia. Ed. The Botanical Society of Lund. 2. Lund, Gleerup.

O´Brien, M.C. and Prendeville, G.N. 1979. Effect of herbicides on cell membrane permeability in Lemna minor. Weed.Res. 19(6): 331-334.

Oorschot, van, J.L.P. 1979. Types of selective action by herbicides which inhibit photosynthesis. Z. Naturforsch. B. 34: 900-904.

Peterson, W.L. and Mayo, J.M. 1975. Moisture stress and its effect on photosynthesis in Dicranum polysetum. Can.J.Bot. 53:2897-2900.

Richard, E.P., Gross, J.R. and Arntzen, C.J. 1979. Glyphosate does not inhibit photosynthetic electron transport and phosphorylation in pea chloroplasts. Weed. Sci. 27(6): 684-688.

Sheirer, D.C. 1980. Differentiation of bryophyte conducting tissues: structure and histochemistry. Bull. Torrey. Bot. Club. 107(3): 289-307.

Stjernquist, I. 1981a. The influence of nutrient and climatic variables on the field CO_2 assimilation of Pleurozium schreberi and Dicranum polysetum and their effect on seasonality of growth. Manuscript, Dept.of Plant Ecol.,Univ. of Lund.

Stjernquist, I. 1981b. Growth and carbon balance of two coniferous forest moss species. Manuscript,Dept.of Plant Ecol.,Univ. of Lund.

Tamm, C.O. 1953. Growth, yield and nutrition in carpets of a forest moss (Hylocomium splendens). Medd. Statens Skogsforskningsinst. 43(1), pp. 140.

Tymonko, J.M. 1979. Studies on the metabolic sites of action of Glyphosate. Diss. Abstr. Int. B. 39(9): 3624-3625.

Whitwell, T., Banks, P., Baster, E. and Santelmann, P.W. 1980. Glyphosate absorption and translocation in Bermuda grass and activity in horsenettle. Weed. Sci. 28(1): 93-96.

Åberg, B. and Eliasson, L. 1978. The herbicidal effects of phenoxy compounds. In: Ramel, C. (ed.) Chlorinated Phenoxy Acids and Their Dioxins. Ecol.Bull. (Stockholm) 27:86-100.

ACKNOWLEDGEMENT

Financial support was given by Skogsvetenskapliga Fonden at the Swedish University of Agricultural Sciences. Areas for field studies were provided by Baroniet Adelswärd AB through B. Mellström, and by Södra Skogsägarna through F. Lönnberg. The manuscript was red and criticized by U. Bärring, N. Malmer, B. Nihlgård and H. Staaf. Assistance in the laboratory work was given by G. Elfversson and the figures were drawn by M. Varga. The authors express their gratitude to all the above-mentioned persons for valuable support and assistance.

Table 1. Effect of herbicide application on CO_2-assimilation and respiration of seven moss species, expressed as percentages of the control value. A = assimilation, R = respiration.

	2,4-D				MCPA				Triclopyr				Glyphosate			
	1 hour		1 month		1 hour		1 month		1 hour		1 month		1 hour		1 month	
	A	R	A	R	A	R	A	R	A	R	A	R	A	R	A	R
Pohlia nutans	82	84	70	119	78	86	70	129	86	73	71	147	88	66	90	147
Hylocomium splendens	83	134	69	115	39	184	33	82	59	176	77	121	83	103	68	95
Pleurozium schreberi	32	175	84	78	-	-	-	-	67	131	87	126	104	19	41	145
Dicranum polysetum	94	161	87	121	-	-	-	-	105	190	111	121	117	57	30	96
Spagnum squarrosum	79	269	81	90	-	-	-	-	69	109	64	149	107	112	152	100
Polytricum commune	96	109	75	97	95	136	87	134	91	140	97	163	95	112	55	108
Rhytidiadelphus loreus	87	109	50	83	100	136	113	106	110	152	110	137	100	94	50	98

Table 2.
Net photosynthetic capacity, expressed as mg $CO_2 \cdot m^{-2} \cdot h^{-1}$, in Pleurozium schreberi and Dicranum polysetum three months and one year after herbicide application.

		Control	2,4-D	Glyphosate		
			Ärtebäck	Kärrstorp	Kungsbäck	Bersbo
Pleurozium	Nov 79	329	132	165	105	253
	Sept 80	329	299	329	204	188
Dicranum	Nov 79	518	606	668	466	456
	Sept 80	518	772	363	637	414

Table 3.
The cover percentage of living part of dominating moss species between July 1979 (a) and September 1980 (b). Spraying with normal dose of 2,4-D occurred in August 1980.

	KÄRRSTORP							
Plot No.	1		2		3		4	
	a	b	a	b	a	b	a	b
Pleurozium schreberi	20	05	30	40	35	30	30	20
Dicranum polysetum	20	25	25	30	15	20	15	20

	ÄRTEBÄCK							
Plot No.	5		6		7		8	
	a	b	a	b	a	b	a	b
Pleurozium schreberi	25	15	25	25	35	25	30	20
Dicranum polysetum	15	20	20	20	20	35	35	25

Table 4.
Relative diurnal net photosynthetic production of a simulated autumn day, 1 month after spraying with normal dose of herbicide. a. Control, b. Glyphosate, c. 2,4-D, d. MCPA, e. Triclopyr. Untreated Dicranum is given the value 1 and used as a reference.

a.	Dicr -	Pleur -	Rhyt -	Spha -	Hylo -	Poly -	Pohl
	1	1.13	1.14	1.27	2.58	3.76	3.88
b.	Dicr -	Pleur -	Rhyt -	Hylo -	Poly -	Spha -	Pohl
	0.09	0.12	0.26	1.56	1.63	2.36	2.81
c.	Rhyt -	Dicr -	Pleur -	Spha -	Hylo -	Pohl -	Poly
	0.30	0.69	0.97	0.98	1.44	2.14	2.61
d.	Hylo -	Rhyt -	Pohl -	Poly			
	0.49	1.33	2.03	2.86			
e.	Spha -	Pleur -	Dicr -	Rhyt -	Hylo -	Pohl -	Poly
	0.36	0.82	1.07	1.08	1.63	1.87	2.89

Table 5.
Relative diurnal net photosynthetic production of simulated summer days one month after herbicide application with 2,4-D. a. autumn, b. June, c. June after a longer period of desiccation, d. August. Untreated Dicranum is given the value 1 and used as a reference.

	Rhyt -	Dicr -	Pleur -	Spha -	Hylo -	Pohl -	Poly
a.	0.30	0.69	0.97	0.98	1.44	2.14	2.61
b.	0.28	0.67	0.98	0.97	1.44	2.11	2.62
c.	0.25	0.64	1.00	0.97	1.45	2.06	2.66
d.	0.28	0.52	1.08	0.94	1.45	1.80	2.85

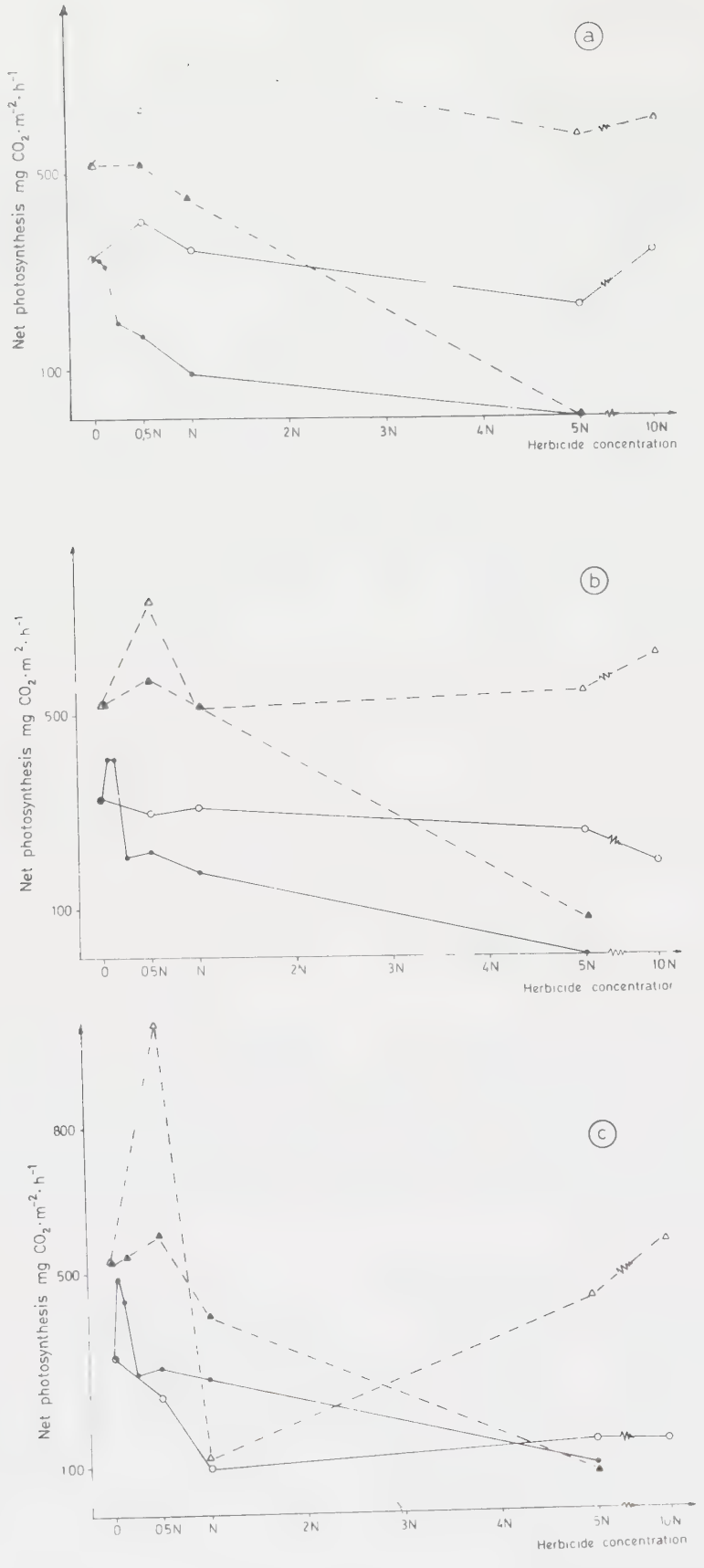


Figure 1. Net photosynthesis of Pleurozium schreberi and and Dicranum polysetum at different herbicide concentrations one hour(a), one week(b) and one month(c) after application.
Symbols: Pleurozium: Glyphosate o, 2,4-D ●.
Dicranum: Glyphosate △, 2,4-D ▲.

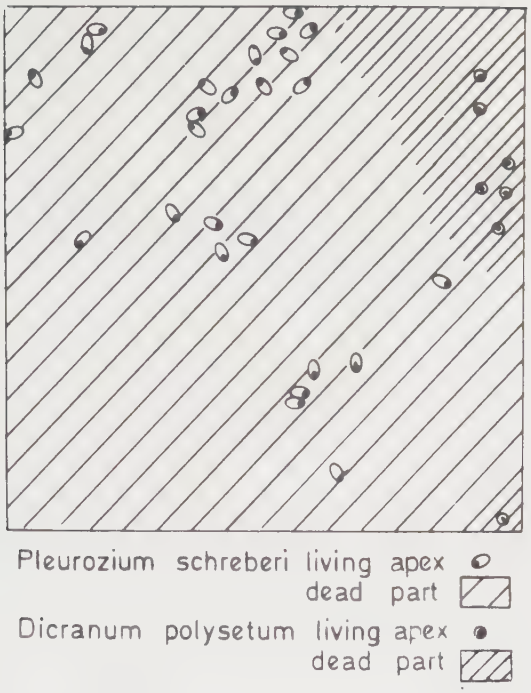


Figure 2. Recovery of moss shoots and parts of shoots one year after treatment with normal dose of 2,4-D. The black dot shows the growing direction. The investigated area is 1 dm^2.

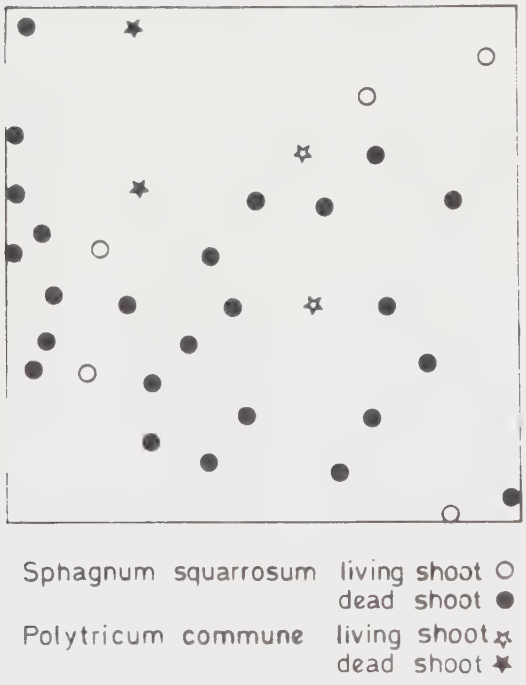


Figure 3. Distribution of living and dead shoot apex in a moss carpet of 1 dm^2 one year after treatment with normal dose of 2,4-D.

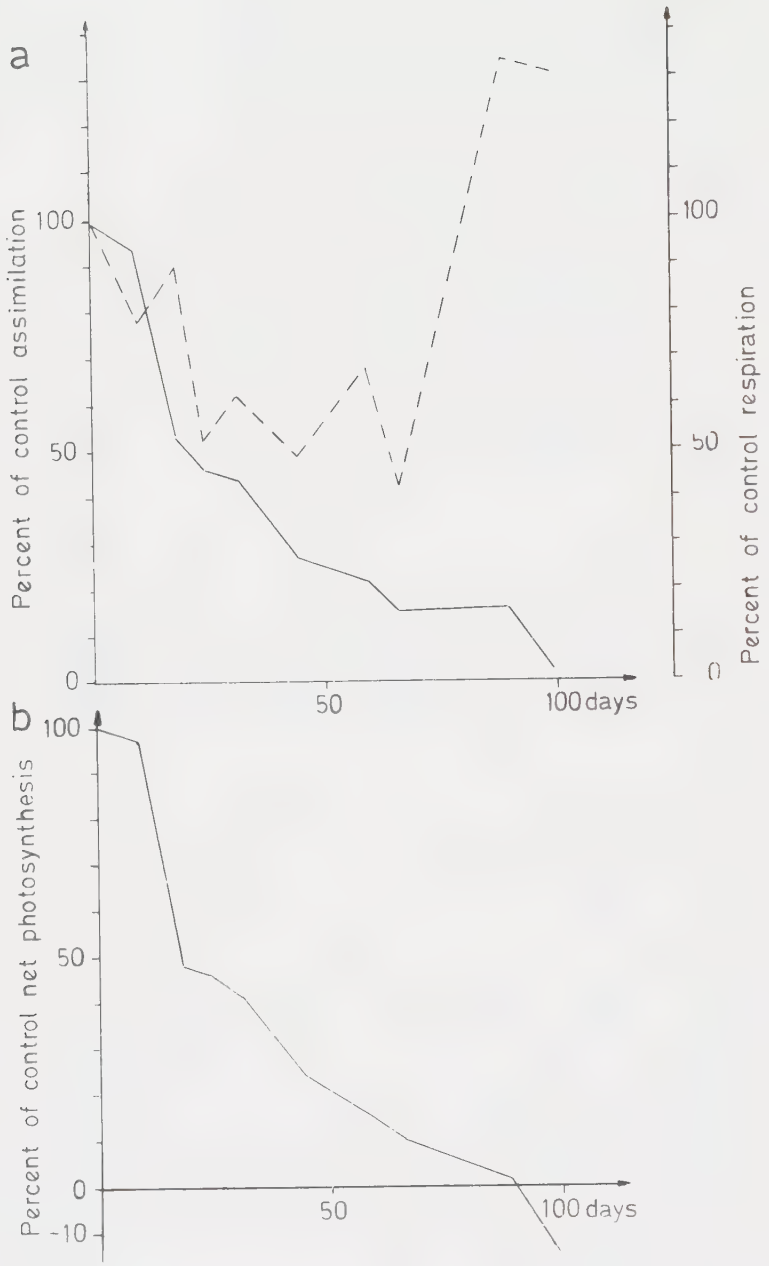


Figure 4. Photosynthetic capacity of Pleurozium shreberi, expressed as percent of control, in relation to the lenght of the growing period in complete darkness.
a. CO_2 assimilation ———, respiration -------.
b. Net photosynthesis ————.

INFLUENCE OF CU AND ZN DEPOSITION ON PHOTOSYNTHESIS AND GROWTH OF TWO MOSS SPECIES

Ingrid Stjernquist

Dept of Plant Ecology
Helgonavägen 5
S-223 62 LUND
Sweden

ABSTRACT

The effect of increased Cu and Zn content in Dicranum polysetum and Pohlia nutans on photosynthesis and respiration was investigated within 8 km of a brass foundry. The moss species were sensitive and non-sensitive respectively to heavy metal pollution.

The Cu+Zn concentrations in shoots nearest to the emittent were 4000+4890 ppm for Pohlia and 97+338 ppm for Dicranum. The assumed background levels were 18+207 ppm and 18+118 ppm respectively. Net photosynthesis of Dicranum was found to increase with distance from the foundry at light intensities above 30 μE $m^{-2}s^{-1}$. Respiration decreased at Cu+Zn concentrations of 54+210 ppm and rose again at 97+338 ppm. The photosynthesis and respiration of Pohlia was inhibited when the heavy metal content in the shoots exceeded 113+475 ppm. The values were then constant at increasing metal concentrations. The effect on growth of the changed photosynthetic ability is discussed for the two moss species.

1 INTRODUCTION

Both coniferous forest mosses and bog mosses are now widely used to determine airborne heavy metal pollution. Common indicator species have been Hylocomium splendens and Pleurozium schreberi (cf. Rühling & Tyler 1970, 1973; Barclay-Estrup & Rinne 1978; Grodzinska 1978), Sphagnum sp. (Pakarinen 1978),but also Dicranum sp. and Leucobryum glaucum (Groet 1976, Pakarinen & Rinne 1980). Compared to the bog mosses, the coniferous forest bryophytes have a higher concentration of heavy metals at identical exposition, depending on their lower annual growth (Pakarinen & Rinne 1980). Possible negative effects of increased metal deposition may therefore be identified at an earlier stage in coniferous mosses.

Some investigations have shown close correlation between increased heavy metal pollution and changes in the presence and coverage of moss species in the bottom layer (Le Blanc et al. 1974, Folkeson 1979). The most sensitive species are reported to disappear near the emittent, but a clearly visible impact, however, first appears when the ecosystem is exposed to heavy fallout of heavy metals or after long exposure.

Johnsen (1976) reported that living moss samples transplanted from background areas to polluted areas showed an increase in heavy metal concentrations, but that the accumulation rate soon levelled off. After three months of exposure the concentrations were almost constant. Thus, if there is a physiological response, e.g. in photosynthesis or respiration, to increased heavy metal exposure, it would appear fairly quickly. Decreased photosynthetic capacity in a bryophyte is likely to lower its vigour and competitive ability against other moss species, leading to reduced growth and possibly to its elimination. Especially in areas with only moderate deposition, effects on photosynthesis could then be discovered much earlier than changes in presence and coverage. At present, however, little experimental evidence for this exists.

The aims of the present experiments were to study: (a) Whether increasing Cu and Zn deposition changes the in situ assimilation rates of Dicranum polysetum and Pohlia nutans; and (b) if so, can the photosynthetic light response of these moss species be related to varying metal contents in the shoot; and finally, (c) do increased concentrations of Cu and Zn have any effects on growth and competition of the two species?

2 MATERIALS AND METHODS

2.1 Site description

The investigation sites were chosen in mature coniferous forests within a distance of 8 km from a brass foundry in the municipality of Gusum, SE Sweden (58°15'N, 16°30'E). The area is heavil affected by airborne heavy metal pollution, especially Cu and Zn but also Pb, Cd and Ni. The foundry, however, emits insignificant amounts of SO_2. The research area has been used for a number of ecological studies, dealing with the effects of Cu and Zn on soil and vegetation (cf. Tyler 1975, Folkeson 1979) and animal populations.

The tree layers of the forests are dominated by pine (Pinus silvestris L.) and spruce (Picea abies (L.) Karst.). Vaccinium myrtillus L., Vaccinium vitis-idea L. and Deschampsia flexuosa (L.) Trin. characterize the field layer. The dominating moss species of the bottom layer are Dicranum polysetum Sw., Hylocomium splendens (Hedw.) Br.Eur., Hypnum cupressiforme Hedw., Pleurozium schreberi (Brid.) Mitt. and Pohlia nutans (Hedw.) Lindb. (Folkeson 1979).

2.2 Material

The two moss species chosen for the investigation, Dicranum polysetum and Pohlia nutans, seem to have different sensitivities to heavy metal pollution, as indicated by their distribution along gradients from the foundry where the species first appear. Dicranum is absent within 2.5 km of the emittent and its frequency increases with the distance. Pohlia, on the other hand, frequently grows close to the foundry (Folkeson, 1979).

2.3 Field experiment

The study was performed in August 1978. Seven experimental plots of 2 x 2 m were placed along a gradient from the foundry and 8 km to the SE (Figure 1). Plot No. 7 was chosen to be the reference site, unaffected by heavy metal deposition from the foundry. All plots were placed on flat ground, in order to avoid influence of metal deposition from other factors than distance, and not less than 100 m from any roads, the nearest being a small gravel road with sparse motor traffic. The lead pollution from the traffic was considered to be insignificant. Within the plots the moss shoots were randomly collected for estimation of the assimilation rate. Each sampling comprised five parallels of each moss species. The assimilation rate was determined 7 times a day as $^{14}CO_2$-incorporation according to Shimshi (1969). The uppermost 1.5 cm of the Dicranum shoots and 2-3 shoots of Pohlia were exposed to $^{14}CO_2$ for 20 seconds and then immediately frozen in liquid nitrogen. Combustion of the samples was accomplished with a Packard Tri Carbonate Sample Oxidizer (Model 306) after dry weight determination (85°C, 24 hours). The radioactivity was measured in a liquid scintillation counter (Intertechnique SL 30).

2.4 Laboratory experiment

Pure carpets of Dicranum and Pohlia were collected from plots Nos. 7 to 3, and 7 and 5 to 1 respectively. From each sample, 2 x 40

Dicranum shoots and 2 x 40 small Pohlia tufts were randomly chosen and placed in plexiglass cuvettes with constant temperature and humidity (15°C and 100% RH).

The density of the moss populations was the same as in situ. Irradiation varied stepwise between 733 and 14 μE $m^{-2}s^{-1}$. Net photosynthesis and dark respiration was registered with gas exchange technique, where CO_2 was detected with an infra red analyser (URAS 2). After the experiment, the dry weight of the mosses was determined (85°C, 24 hours).

The standard deviation of photosynthesis and respiration rates, as measured on a weight basis in different experimental cuvettes with the gas exchange technique, was determined to be 9% and 12% respectively of the mean value (n=9) in a separate study (Stjernquist and Ingelög 1981). Each cuvette contained 40 shoots.

2.5 Calculations and statistics

A one-way analysis of variance was used to test the influence of heavy-metal concentrations (Σ Cu+Zn) (independent variable) on photosynthesis of Dicranum and Pohlia (dependent variable).

Possible changes in irradiation response of the photosynthesis with increasing Cu+Zn concentration was estimated with Student's t-test. An estimation was made of the divergence from zero of the slope of the linear regression between the light response slope and the logarithm of the Cu+Zn concentration in the moss tissue. Student's t-test was also used to test the difference in photosynthesis between two experimental plots.

The diurnal CO_2 assimilation of Dicranum and Pohlia on the seven experimental plots was estimated from the regression equations in Table 3. The irradiation conditions of plot No. 3 on August 16 were chosen. The values were calculated by interpolation between the measurement points and integration of the area under the resulting graphs.

3 RESULTS

3.1 Heavy metal contents in mosses

Along the gradient, the highest heavy metal concentration in the shoot was found for Zn, the values increasing three-fold for Dicranum from plot 7 (118 ppm) to plot 3 (338 ppm) and 24-fold for Pohlia from plot 7 (207 ppm) to plot 1 (4890 ppm) (Table 1). The Cu content in the bryophytes was constantly lower, but the increase was steeper: 5-fold for Dicranum and over 200-fold for Pohlia. With the exception of Pohlia on plots 1 and 2, the changes in Pb concentration were small. A maximum value of 250 ppm was registered near the foundry. The Ni and Cd content in the shoots was very low for both moss species and about the same in all plots.

3.2 The importance of distance

The visual appearance of Pohlia was unchanged along the gradient (Figure 2). On plot 3 about 1-1.5 cm of the youngest tissue of Dicranum was green. Older parts were brown and pressed down parallel to the ground. Even the matured leaves on the green segment of the shoots had brown spots at the ends. On the other plots, the Dicranum populations were normal in appearance. When all the light intensities were included, the analysis of variance showed that the distance from the foundry might not significantly influence the assimilation rate of Pohlia (Table 2). For Dicranum, however, there was an effect, though only significant at constant climatic conditions.

3.3 Photosynthetic reaction to increased light intensity

During the experimental period, the weather was typical for clear summer days, with high irradiation and air temperature and decreasing relative humidity during the day (Figure 3). Maximum irradiation was 1700 $\mu E\ m^{-2}s^{-1}$. The seven plots were not equally exposed, however. The relative humidity on plots 4 and 5 maintained a high value during the first day, while on plots 2, 3 and 7 it dropped down to 40% at noon. The temperature at the top of

the moss carpet varied between 9°C at sunrise and 25°C in the middle of the day.

The in situ assimilation rate of Dicranum and Pohlia along the gradient measured as CO_2 incorporation was in all cases positively linearly related to the logarithms of irradiation (Table 3). When using non-transformed values, the fit was less significant. For Dicranum the assimilation response to light intensity seemed to decrease in the order 4-7-6-5-3, but the slopes of the response curves were not statistically significantly separated. The CO_2 fixation of Pohlia can be separated into three groups - 1,3,7/ 2,5/ 4,6 - showing a significant increase in assimilation in that order ($p < 0.05$).

At constant climatic conditions in the laboratory, using light intensities above 70 $\mu E\ m^{-2}s^{-1}$, the CO_2 exchange of Dicranum from plots 5 to 3 was significantly ($p < 0.05$) reduced as compared to that from the reference site (No. 7) (Figure 4a). Samples from plot 4 again had a higher photosynthetic rate than those from plot 5 ($p < 0.05$), at irradiation above 190 $\mu E\ m^{-2}s^{-1}$. At low irradiation, 30 $\mu E\ m^{-2}s^{-1}$ and 14 $\mu E\ m^{-2}s^{-1}$ the net photosynthesis decreased for plots 5 and 3. The dark respiration rate of Dicranum from plots 5 and 4 was inhibited ($p < 0.05$), but then again rose on plot 3 ($p < 0.05$) (Figure 4b).

When Pohlia was exposed to light intensities above 70 $\mu E\ m^{-2}s^{-1}$, the net photosynthesis seemed to decrease in the order 7-5-4-3 (Figure 5a). The difference was significant ($p < 0.05$) between plots 7 and 3 for all light intensities, and at 72 $\mu E\ m^{-2}s^{-1}$ and 733 $\mu E\ m^{-2}s^{-1}$ also between samples from plots 7 to 4 and 4 to 3. Samples taken closer to the foundry had a photosynthetic activity similar to that of plot 3. At 14 $\mu E\ m^{-2}s^{-1}$, positive CO_2 exchange existed only on plots 7 to 4. The dark respiration rate of Pohlia was inhibited on plots 3 to 1 compared to the reference site ($p < 0.05$).

The photosynthetic light response, expressed as the slope of the exponential regression of photosynthetic rate on light intensity, is negatively correlated with increasing concentrations of Cu+Zn in the laboratory experiment, but significantly so only for

Dicranum ($p < 0.05$) (Table 4, Figure 6). In the in situ experiment, however, none of the species showed significantly changed light response.

Assuming identical irradiation conditions on the plots over a day, the diurnal CO_2 incorporation and production would be as illustrated in Figure 7. Pohlia has no regular pattern, the highest figures being on plots 4 and 6. The CO_2 fixation of Dicranum decreased from the reference site to plot 5, then rose on plot 4 and then again decreased on plot 3.

4 DISCUSSION

4.1 The method

The photosynthetic and dark respiration reactions of Dicranum and Pohlia at different distances from the brass foundry may be an isolated effect of variations in the Cu+Zn concentrations of the shoots. Of the other heavy metals identified in the mosses, Ni and Cd had small and equal values and may not have influenced the photosynthetic process. On the experimental sites more than 3 km away from the emittent, the lead content is considered to be of the same magnitude as the background level. Pakarinen & Rinne (1980), for example, reported a value of 27 ppm Pb for Dicranum majus in some background areas in southern Finland. However, Dicranum elongatum at the Stordalen area in the north of Sweden contains a very low value, 6 ppm Pb in the top segment of the shoots (Malmer & Nihlgård 1980). The increased Pb concentration in Pohlia near the foundry will probably not change the CO_2 fixation significantly, as earlier investigations have shown that Pb tolerance in mosses seems to be rather high. Simola (1977) found no decrease in growth when Sphagnum nemorum was cultivated in long-term experiments in 0.01 M Pb solution, and Brown & Bates (1972) working with Grimmia doniana reported no negative reactions of photosynthesis up to a lead content of 1000 ppm.

The assimilation capacity of bryophytes growing in tufts like Dicranum and Pohlia seems to be dependent primarily on irradiation and secondarily on relative humidity (cf. Stjernquist 1981a). Since irrigation was performed before each assimilation determination in situ, the regulating effect of decreased humidity is assumed to be insignificant.

The temperature range at the top of the moss carpet during the experimental period, 9-25°C, probably does not affect the assimilation rate (cf. Källomäki & Hari 1976), and therefore changes found in photosynthetic response to a certain light intensity may reflect an influence of the metal concentration.

4.2 The influence of Cu and Zn on photosynthesis

Dicranum

At constant irradiation and temperature and a relative humidity of 100%, the CO_2 assimilation of Dicranum - expressed as net photosynthesis plus dark respiration, significantly decreases with increasing Cu+Zn concentration. In the in situ investigation, however, no clear relationship is discerned. Two factors may be of importance to the difference. Firstly, the low air humidity during the experimental period with values down to 30% RH caused a high rate of evaporation from the moss carpet, and in spite of irrigation the moss shoots probably lost enough water to reduce the assimilation. Especially plots 7 and 3 showed a large number of hours with low relative humidity. Secondly, the growth form of Dicranum causes a heavy-metal deposition primarily in the outermost parts of the leaves, and because transport within the moss tissue is reported to be insignificant (cf. Coombes & Lepp 1974) the basal parts may be less affected. The field method used implies that all segments of the shoots are equally illuminated, which tends to overestimate the photosynthetic capacity as expressed per unit of dry weight. If the in situ assimilation along the metal gradient is adjusted for the discussed factors, light response on the different plots will probably approach the situation shown by the laboratory results.

The negative influence of the Cu+Zn level on net photosynthesis of Dicranum evident at light intensities above 70 µE $m^{-2}s^{-1}$ is probably not significant until the Cu+Zn concentrations reached are three-fold and two-fold the background level respectively, i.e. about 50 ppm and 200 ppm (plot No. 5). The capacity of the Dicranum sporophyte to tolerate this level may be related to the ability of the mosses to immobilize the cations in cell walls by ion exchange and by chelate bonds (cf. Rühling & Tyler 1970, Simola 1977). Cu is reported to exert toxic effects at much lower concentrations than Zn (Coombes & Lepp 1974). Thus, while Cu at 6 ppm causes inhibition in growth of Marchantia, a level of 100 ppm of Zn is needed to cause the same effect. Pickering & Puia (1969), however, could not show any toxic effect of Zn on Fontinalis antipyretica. The great Zn tolerance in mosses may probably be due to the fact that a high percentage of the absorbed Zn ions is bound in the cell walls, even with a high heavy metal concentration in the shoots. Burton & Peterson (1979), for example, found that about 80% of the Zn ions were bound in that way at concentrations around 2500 ppm in Fontinalis and 3500 ppm in Solenostoma.

The variations in assimilation capacity with increasing Cu and Zn content may be the joint result of two different dose-response relations. At higher Cu content, as compared to the background level (plot 7), the assimilation rate of Dicranum decreases continuously, while Zn is assumed not to cause metabolical disturbances at values below 280 ppm. The significantly higher net photosynthesis at light intensities above 193 µE $m^{-2}s^{-1}$ when moving along the gradient from plot 5 to 4 indicates that changed Zn concentrations from 210 to 280 ppm at least do not hamper the CO_2 uptake of Dicranum, since the Cu content in shoots on the two sites is almost the same. The nearly complete inhibition of net photosynthesis closer to the foundry is probably an effect of increased Cu concentration. The additional influence of the higher Zn content cannot be isolated with the utilized in situ sampling method.

The respiration rate of Dicranum is reduced at the same Cu+Zn concentration as net photosynthesis. The brown spots on the annual shoots on plot 3 may be exposed to decomposer activity, which contributes to the increased respiration here.

Pohlia

When the two moss species are exposed to the same Cu+Zn deposition within 3.6 km from the emittent, Pohlia absorbs greater amounts of heavy metals than Dicranum. A possible explanation of this phenomenon could be a slower growth of the Pohlia shoots (cf. Pakarinen & Rinne 1980). The photosynthetic process of Pohlia, however, probably is much more tolerant to the Cu+Zn pollution than that of Dicranum. The highest Cu content in healthy Pohlia populations has earlier been found in a swamp forest in Canada, where the moss shoots contained $35 \cdot 10^5$ ppm (Dykeman & de Sousa 1966). The heavy metal tolerance of Pohlia may be related to the very thick cell walls, especially at the tops of the leaves (Nyholm 1954-69), which are the most exposed to deposition.

Yet an increased Cu+Zn content in the moss tissue from the background level to 113+475 ppm seems to influence the photosynthetic capacity of Pohlia negatively at light intensities above 70 $\mu E \cdot m^{-2} s^{-1}$. When the metal concentrations exceed this value, the net photosynthesis in this bryophyte remains unaffected up to at least 4000+4890 ppm Cu+Zn. No changed property of the photosynthetic apparatus that may bring about the compensation for the heavy metal effect has been identified in this investigation.

The three significantly separated groups of plots with similar light response found in the in situ experiment diverge from the Cu+Zn gradient and the laboratory results. A reason contributing to the result may be that the low air humidity during most of the day at plots 3 and 7 caused a high evaporation rate, and the net photosynthesis of Pohlia could therefore be inhibited in spite of irrigation.

4.3 Growth of Dicranum and Pohlia

The estimated diurnal production of Dicranum and Pohlia along the gradient, at good water conditions, did not seem to be exceptionally low. Diurnal CO_2 incorporation of Dicranum in the background area, for example, was of the same magnitude as for irrigated populations in an unpolluted pine forest in Central Sweden (Stjernquist 1981a). However, Folkeson (1979), studying the frequency of the moss species in the area around Gusum, found decreasing values for Dicranum already at a distance from the foundry corresponding to plot 5. For Pohlia, however, no such tendency was noted within a distance of 6 km from the emittent.

In combination with a negative impact of Cu and Zn on the net photosynthesis of a certain moss species, its specific reaction to climatic variables may be important for survival in polluted areas. The laboratory experiment indicated that when Dicranum and Pohlia are exposed to increased Cu+Zn deposition, both bryophytes seem to require higher light intensity for positive CO_2 exchange, compared to the reference site. Considering the habitats where the two moss species grow, this characteristic together with the decreased photosynthetic capacity will probably have different effects on growth and competition of Dicranum and Pohlia respectively. Dicranum grows in coniferous forests and is often found in pure carpets in shaded and relatively dark habitats. In spite of the fact that the assimilation rate may be controlled mainly by irradiation, even unpolluted shoots seem to be unable to utilize high light intensities (Stjernquist 1981a). Compared to the mosses co-existing with Dicranum on the forest floor, the growth of this bryophyte will probably be favoured by decreased irradiation. A Cu+Zn pollution may then reduce the diurnal CO_2 fixation, especially in autumn when water conditions are at an optimum for growth. Decreased production possibly causes a negative influence on the competitive ability of the species (cf. Stjernquist 1981b). It is likely that the formation of brown spots on the youngest shoot tissue contributes to the low vigour of Dicranum on plot No. 3. Similar effects on the

vegetation have been reported to appear in the middle of summer around a zinc smelter in New Jersey, USA (Buchauer 1973).

Pohlia, however, seems to be a colonist species (cf. During 1979), growing in exposed habitats with high irradiation. An inhibited photosynthetic capacity at Cu+Zn concentrations about 110+480 ppm will decrease the vigour of the moss but probably does not affect the distribution because of the weak competition from other species in heavily polluted areas.

5 REFERENCES

Barclay-Estrup, P. and Rinne, R.J.K. 1978. Lead and zinc accumulation in two feather mosses in northwestern Ontario, Canada. Oikos 30:106-108.

Brown, D.H. and Bates, J.W. 1972. Uptake of lead by two populations of Grimmia doniana. J. Bryol. 7:187-193.

Buchauer, M.J. 1973. Contamination of soil and vegetation near a zinc smelter by zinc, cadmium, copper and lead. Environ. Sci. Technol. 7(2):131-135.

Burton, M.A.S. and Peterson, P.J. 1979. Studies on zinc localization in aquatic bryophytes. Bryologist 82(4):594-598.

Coombes, A.J. and Lepp, N.W. 1974. The effect of Cu and Zn on the growth of Marchantia polymorpha and Funaria hygrometrica. Bryologist 77:447-452.

Dykeman, W.R. and De Sousa, A.S. 1966. Natural mechanisms of copper tolerance in a copper swamp forest. Can.J.Bot. 44:871-878.

During, H.J. 1979. Life strategies of bryophytes: A preliminary review. Lindbergia 5(1):2-18.

Folkeson, L. 1979. Interspecies calibration of heavy-metal concentrations in nine mosses and lichens: - Applicability to deposition measurements. Water Air Soil Pollut. 11:253-260.

Grodzinska, K. 1978. Mosses as bioindicators of heavy metal pollution in Polish national parks. Water Air Soil Pollut. 9:83-97.

Groet, S.S. 1976. Regional and local variations in heavy metal concentrations of bryophytes in the northeastern United States. Oikos 27:445-456.

Johnsen, I. 1976. Problems in relation to the use of plants as monitors of air pollution with metals. In Kärenlampi, L. (ed.) Proceedings of the Kuopio Meeting on Plant Damages caused by Air Pollution. Kuopio, pp. 110-114.

Kellomäki, S. and Hari, P. 1976. Rate of photosynthesis of some forest mosses as a function of temperature and light intensity and effect of water content of moss cushion on photosynthetic rates. Silva Fenn. 10(4):288-295.

Le Blanc, F., Robitaille, G. and Rao, D.N. 1974. Biological response of lichens and bryophytes to environmental pollution in the Murdockville copper mine area, Quebec. J. Hattori Bot. Lab. 38:405-433.

Malmer, N. and Nihlgård, B. 1980. Supply and transport of mineral nutrients in a sub-arctic mire. In: Sonesson, M. (ed.) Ecology of a subarctic mire. Ecol. Bull. (Stockholm) 30:63-95.

Nyholm, E. 1954-69. Musci.In:Illustrated Mossflora of Fennoscandia. Ed. The Botanical Society of Lund.2. Lund. Gleerup, 799 pp.

Pakarinen, P. 1978. Distribution of heavy metals in the Sphagnum layer of hummocks and hollows. Ann.Bot.Fenn. 15:287-292.

Pakarinen, P. and Rinne, R.J.K. 1980. Growth rates and heavy metal concentration of five moss species in paludified spruce forests. Lindbergia 5:77-83.

Pickering, D.C. and Puia, I.L. 1969. Mechanism for the uptake of zinc by Fontinalis antipyretica. Physiol. Plant. 24:232-234.

Rühling, Å. and Tyler, G. 1970. Sorption and retention of heavy metals in the woodland moss Hylocomium splendens (Hedw.) Br. et Sch. Oikos 21:92-97.

Rühling, Å. and Tyler, G. 1973. Heavy metal deposition in Scandinavia. Water Air Soil Pollut. 2:445-455.

Shimshi, D. 1969. A rapid field method for measuring photosynthesis with labelled carbon dioxide. J.Exp.Bot. 20:381-401.

Simola, L.K. 1977. The effect of lead, cadmium, arsenate and fluoride ions on the growth and fine structure of Sphagnum nemorum in aseptic culture. Can.J.Bot. 55:426-435.

Stjernquist, I. 1981a. The influence of nutrient and climatic variables on the field CO_2 assimilation of Pleurozium schreberi and Dicranum polysetum and their effect on seasonality of growth. Manuscript, Dept. of Plant Ecol., Univ. of Lund.

Stjernquist, I. 1981b. Growth and carbon balance of two coniferous forest moss species. Manuscript Dept. of Plant Ecol., Univ. of Lund.

Stjernquist, I. and Ingelög, T. 1981. Effects of silvicultural herbicides on the photosynthesis of seven bryophyte species. Manuscript, Dept. of Plant Ecol., Univ. of Lund.

Tyler, G. 1975. Effects of heavy metal pollution on decomposition in forest soil. SNV PM 443E, 542E. National Swedish Environment Protecting Board.

ACKNOWLEDGEMENTS

I want to express my gratitude to Prof. N. Malmer, Dept. of Plant Ecology, University of Lund, for valuable advice and discussions. I also would like to thank the following persons for helpful support and critisism: L. Folkeson, H. Staaf, S. Söderlund and M. Varga.

Table 1.

Concentration of Cu+Zn in shoots of *Pohlia nutans* and *Dicranum polysetum* on experimental plots 1-7 and the distance from the brass foundry

Plot no.	1	2	3	4	5	6	7
Distance, m.	130	350	3050	3350	3600	5400	7800
Pohlia							
Cu ppm	4000	480	113	84	61	32	18
Zn ppm	4890	1200	475	348	295	191	207
Pb ppm	247	100	73	67	50	50	37
Ni ppm	8	6	5	5	4	5	3
Cd ppm	2	2	2	1	1	1	1
Dicranum							
Cu ppm	-	-	97	58	54	32	18
Zn ppm	-	-	338	280	210	162	118
Pb ppm	-	-	35	49	33	42	23
Ni ppm	-	-	3	4	3	3	2
Cd ppm	-	-	1	1	1	1	1

Table 2.

Influence of distance from the brass foundry of experimental plots 1-7 on the assimilation rates of *Pohlia nutans* and *Dicranum polysetum*, estimated with analysis of variance. The analysis comprises all sampling occasions during three days in the field experiment and all light intensities in the laboratory experiment.

	F-ratio	Significance
Pohlia		
Field experiment	1.17	>0.05
Lab. experiment	1.20	>0.05
Dicranum		
Field experiment	0.74	>0.05
Lab. experiment	7.78	0.01 > p >0.001

ble 3.

near regression analysis between irradiation (independent variable), asured as $\mu E \cdot m^{-2} s^{-1}$, and assimilation rate (dependent variable), ex- essed as mg CO_2.g $dw^{-1} \cdot h^{-1}$, on experimental plots 1-7. The regression uation is y=k lnI+l. The correlation coefficient (r) and the signi- cance (p) is given for each plot.

hlia	k	l	r	p
ot no.				
	-0.44	0.50	0.96	0.001
	-0.71	1.68	0.90	0.01
	-0.41	0.65	0.83	0.001
	-1.11	2.55	0.95	0.001
	-0.60	0.73	0.74	0.01
	-1.08	2.46	0.97	0.001
	-0.44	0.69	0.87	0.001
icranum				
lot no.				
	-0.33	0.55	0.85	0.001
	-0.49	1.00	0.94	0.001
	-0.37	0.69	0.83	0.001
	-0.37	0.62	0.94	0.001
	-0.43	0.80	0.76	0.01

able 4.

inear regression analysis between the light response of assimi- ation rate (dependent variable), expressed as the slope of the egression, and the Cu+Zn concentration (independent variable), xpressed as ppm, in Pohlia nutans and Dicranum polysetum. The re- ression equation is y=k x+l. The correlation coefficient (r) and he significance (p) is given.

ohlia	k	l	r	p
ield exp.	-0.06	1.08	0.30	>0.05
ab. exp.	-0.03	0.54	0.42	>0.05
icranum				
ield exp.	-0.03	0.56	0.21	>0.05
ab. exp.	-0.36	2.31	0.91	0.05 > p >0.01

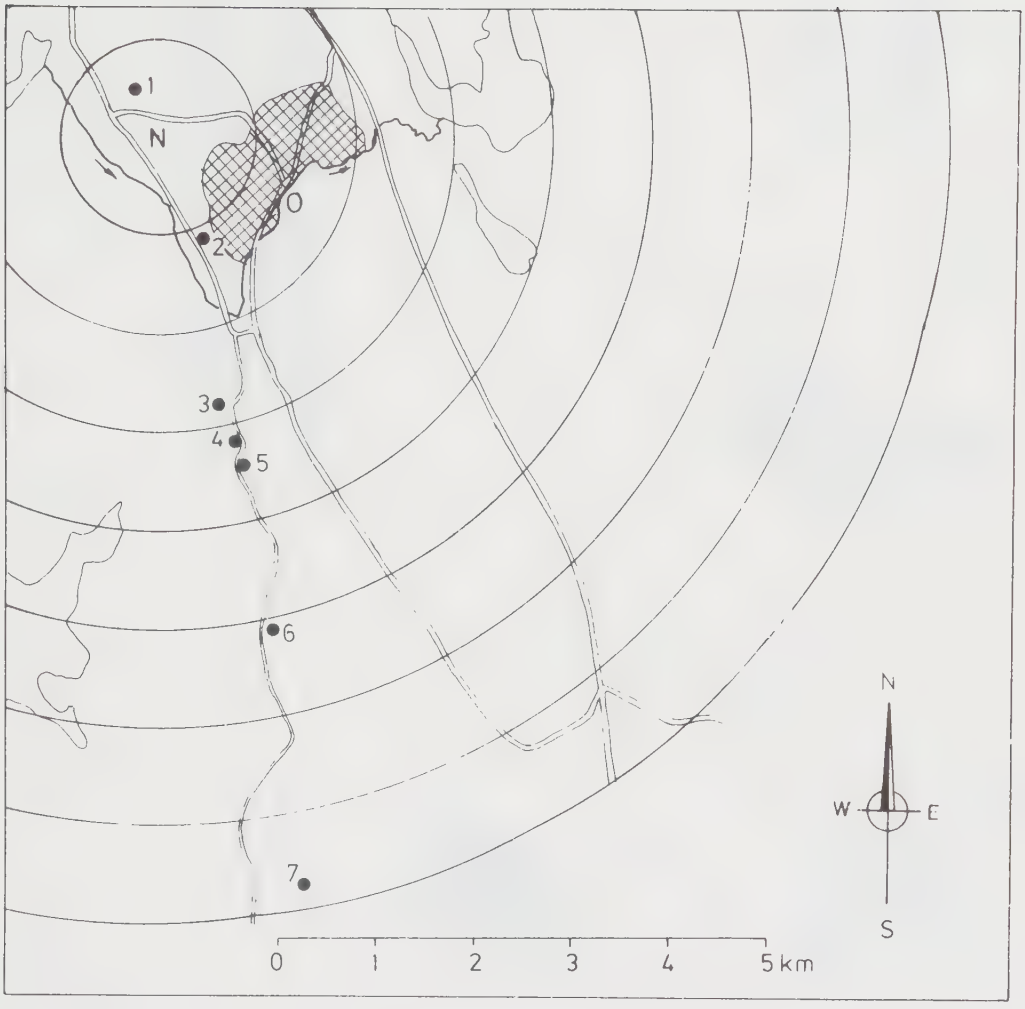


Figure 1. The investigation area and the position of the experimental plots around the new (N) and old (O) brass foundry at Gusum.

DICRANUM POLYSETUM

Plot 3

Plot 4-7

POHLIA NUTANS

Plot 1-7

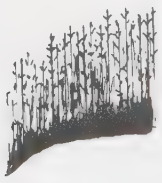


Figure 2.The morphological appearance of Dicranum polysetum and Pohlia nutans on plots Nos. 1-7.

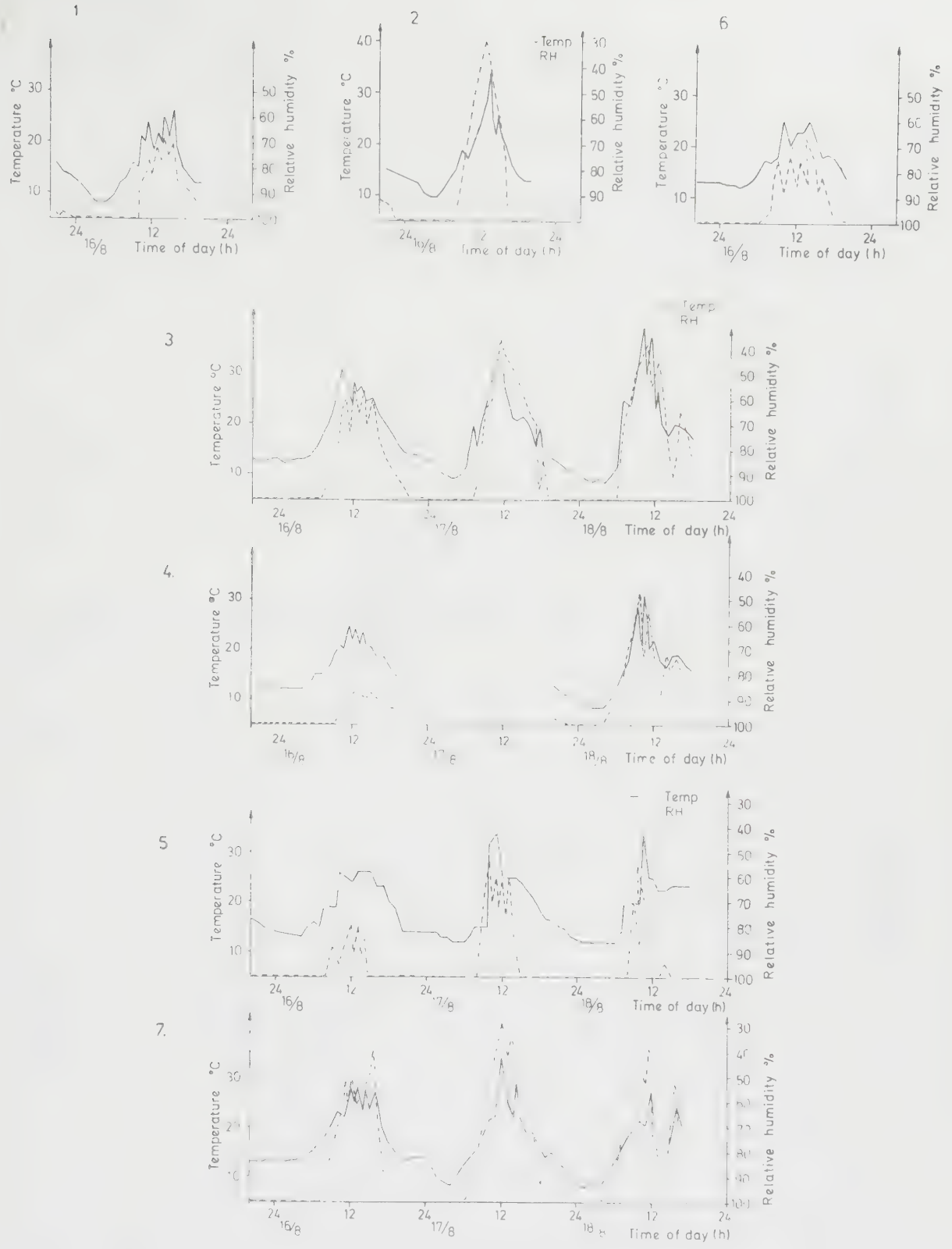


Figure 3.Temperature and relative humidity on plots Nos. 1-7 during the investigation period in August 1978.

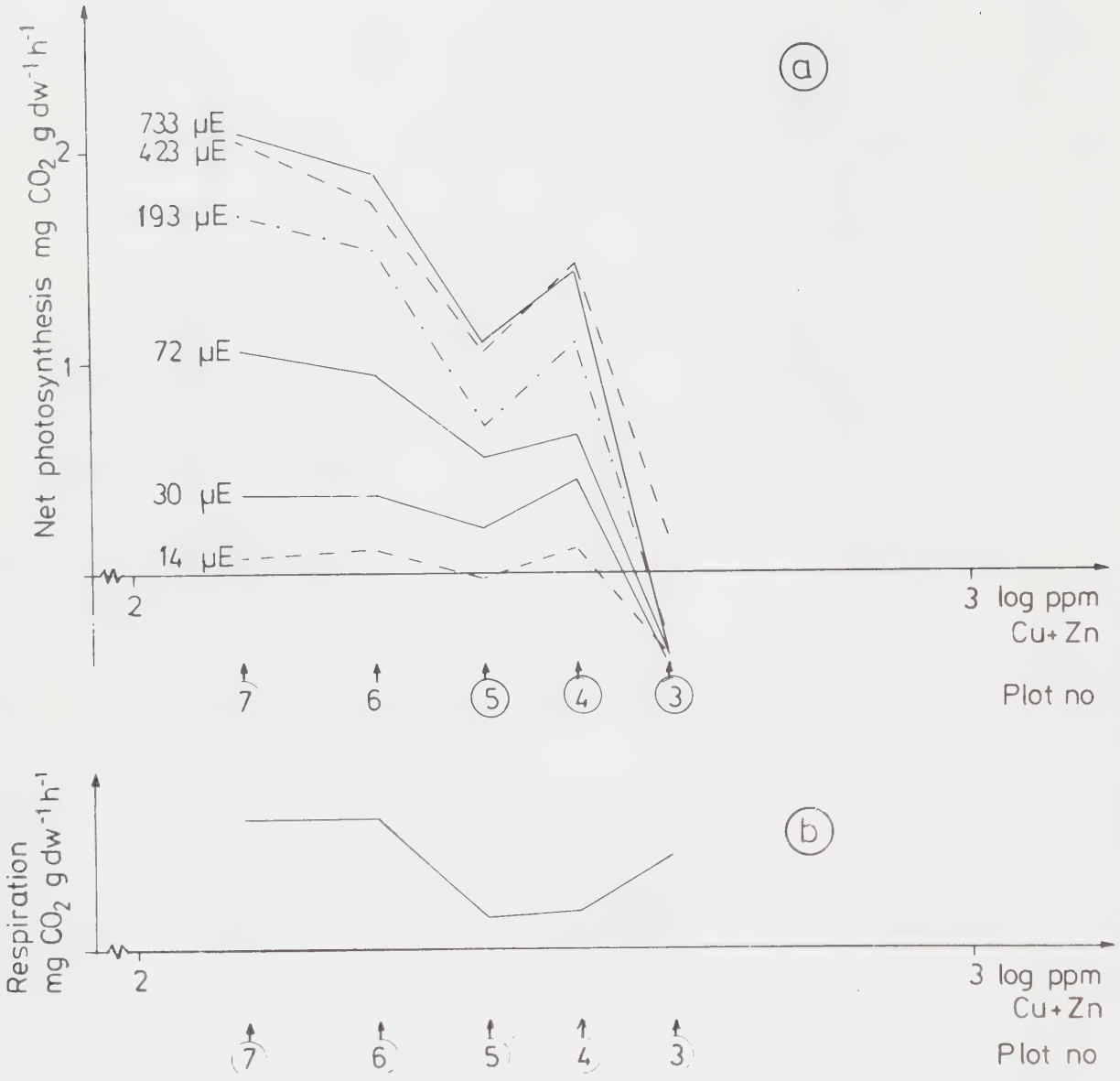


Figure 4a. The relationship between net photosynthesis of Dicranum polysetum and the Cu+Zn concentration in the shoots at six different light intensities. Plots Nos. 1-7 are marked on the x-axis.

4b. The relationship between respiration of Dicranum polysetum and the Cu+Zn concentration in the shoots. Plots Nos. 1-7 are marked on the x-axis.

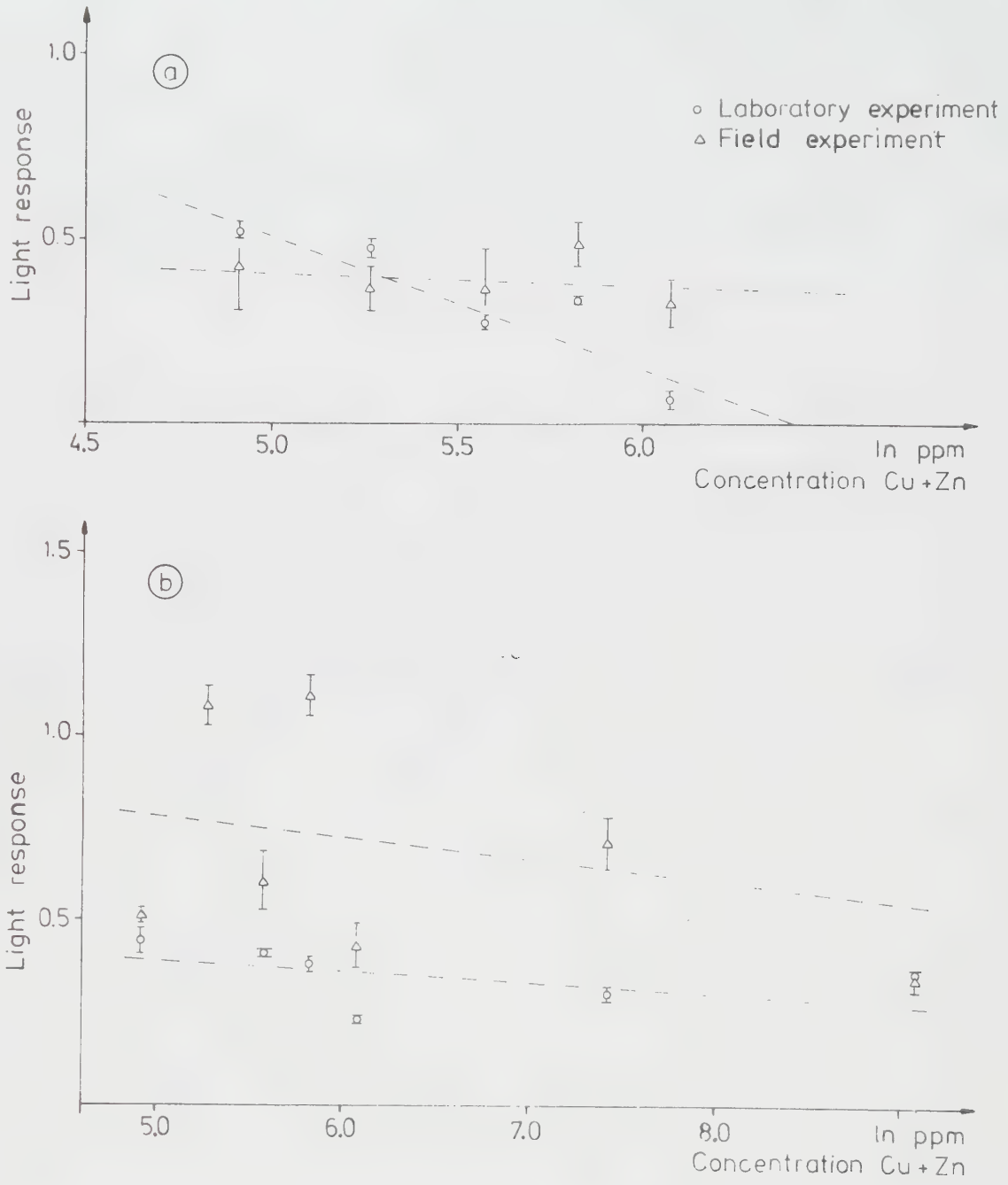


Figure 6. The relationship between the Cu+Zn concentration in Dicranum polysetum and Pohlia nutans and the light response of CO_2 assimilation.
Symbols: Dicranum o. Pohlia Δ.

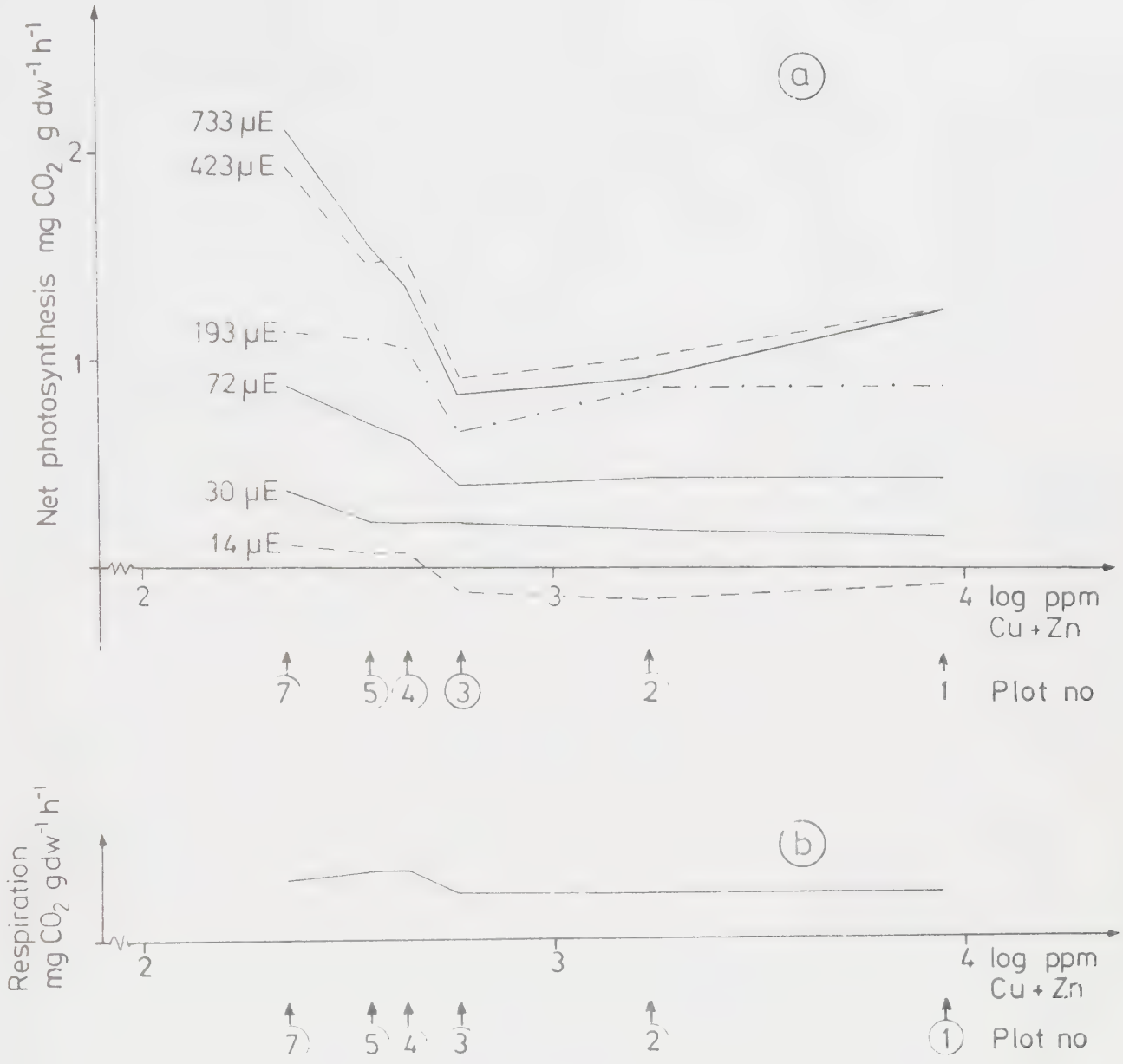


Figure 5a. The relationship between net photosynthesis of Pohlia nutans and the Cu+Zn concentration in the shoots at six different light intensities. Plots Nos. 1-7 are marked on the x-axis.

5b. The relationship between respiration of Pohlia nutans and Cu+Zn concentration in the shoots. Plots Nos. 1-7 are marked on the x-axis.

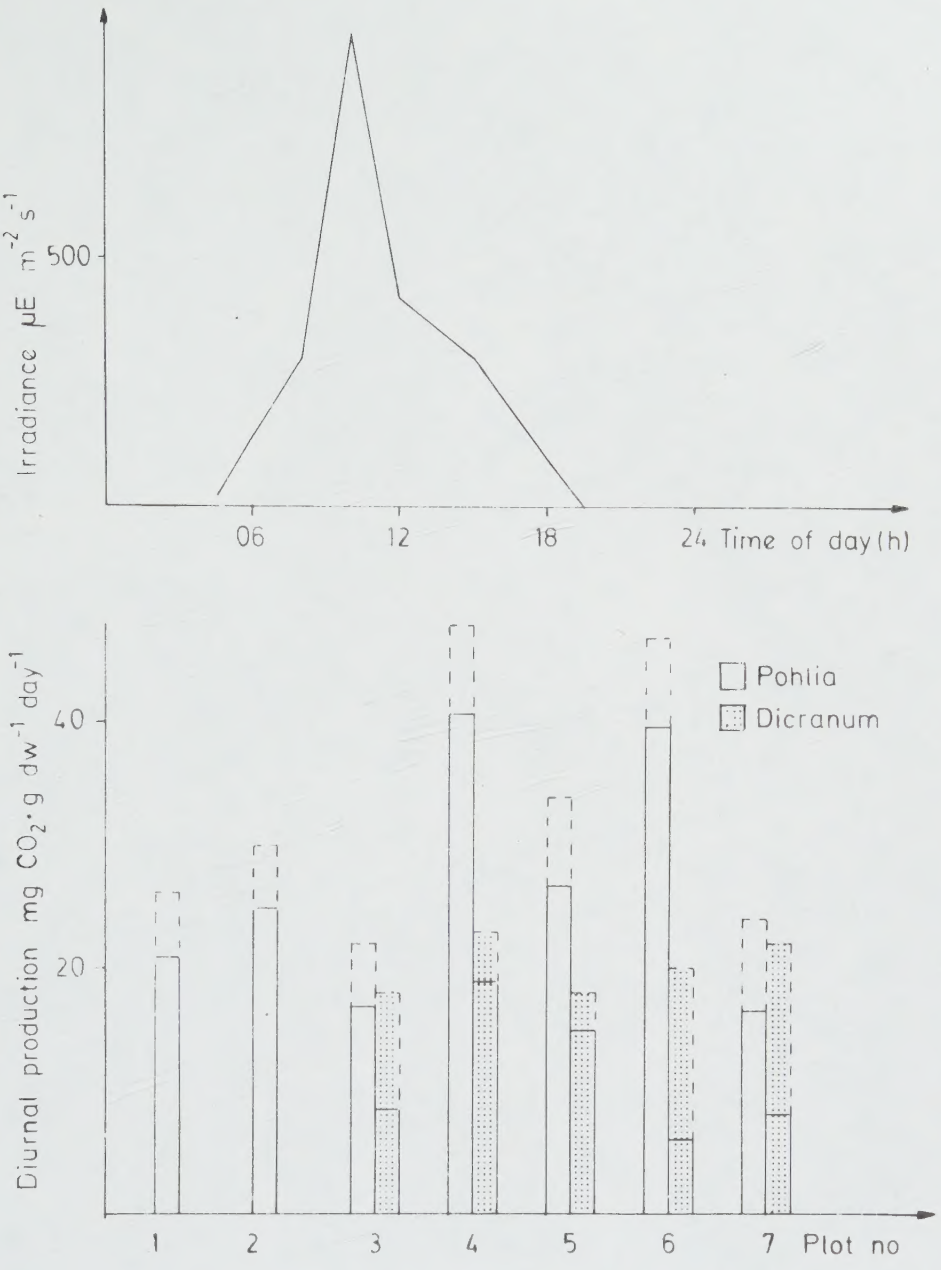


Figure 7. Diurnal CO_2 incorporation on plots Nos. 1-7 at a simulated irradiation corresponding to plot No. 3 on August 16, 1978. Respiration levels are marked with broken lines.